Cyclical succession in semi-arid savannas revealed with a spatial simulation model

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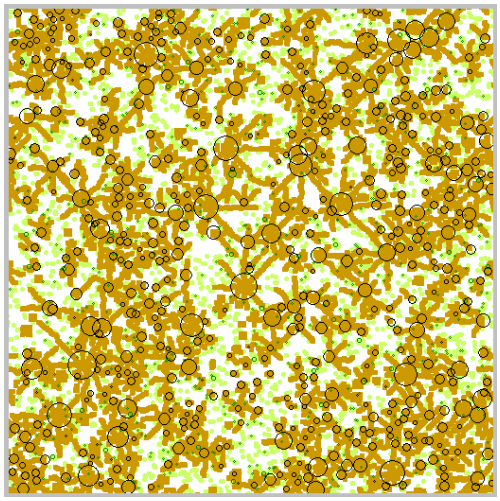

A model should be as simple as possible.
But no simpler.

Albert Einstein

I proceeded with the utmost caution, but, with all my care, a small twig caught hold of my sleeve. While thinking to disengage it quietly with the other hand, both arms were seized by these rapacious thorns, and the more I tried to extricate myself, the more entangled I became; till at last it seized hold of the hat also; (…) In revenge for this ill-treatment, I determined to give the tree a name which should serve to caution future travellers against allowing themselves to venture within its clutches.

W.J. Burchell (1782-1863) about *Acacia mellifera ssp. detinens*
*(*detinere, *Lat.* = to detain*)*

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1
Introduction

Savannas are characterized by the coexistence of two contrasting life forms, grasses and woody species[1]. They cover an eighth of the terrestrial global surface and are of major socio-economic importance in temperate and tropical regions (Scholes & Archer 1997). A large and growing proportion of the world's human population is dependent on savannas as rangelands for their livestock (Scholes & Archer 1997). Worldwide, the ecological and economic function of savannas is threatened by shrub encroachment, i.e. the increase of woody species often unpalatable to livestock at the expense of the grass layer (Smit 2004). Many theories have been put forward to explain tree-grass coexistence and the ongoing shrub encroachment in savannas. According to Sankaran *et al.* (2004), these theories can be classified as competition-based mechanisms (*e.g.*, Walter 1971; Walker *et al.* 1981; Walker & Noy-Meir 1982; Eagleson & Segarra 1985; Sala *et al.* 1997; Fernandez-Illescas *et al.* 2001; van Langevelde *et al.* 2003) or demographic bottleneck-models (*e.g.*, Hochberg *et al.* 1994; Jeltsch *et al.* 1996; Jeltsch *et al.* 1998b; Higgins *et al.* 2000; Jeltsch *et al.* 2000; van Wijk & Bouten 2001).

Walter's (1971) two-layer hypothesis is a prominent example of a competition-based approach that explains tree-grass coexistence with a niche separation mechanism. The two-layer hypothesis assumes that trees have access to deeper soil layers than grasses for water uptake. Thereby, intra-life form competition is spatially concentrated relative to inter-life form competition which leads to coexistence. In the two-layer-framework, shrub encroachment results from increased availability of water in deeper soil layers due to reduced grass cover, which is mainly caused by overgrazing. However, empirical and theoretical evidence for the two-layer hypothesis is equivocal. For instance, tree-grass coexistence is also reported from a field site in Namibia where the soil is too shallow to allow for a rooting niche separation (Wiegand *et al.* 2005). Another issue which cannot be explained by the two-layer hypothesis is the recruitment phase when the roots of tree seedlings overlap and compete directly with grass roots

[1] In this dissertation, the term "grass" will be used as a short-hand expression for grasses and forbs while the term "tree" will be used as a synonym for woody species in general if not stated differently.

(Sankaran *et al.* 2004). Other competition-based mechanisms include phenological niche separation based on temporal separation of the regeneration niches of trees and grasses (Sala *et al.* 1997; Scholes & Archer 1997; House *et al.* 2003), a hydrologically driven model based on the trade-off between competitive ability and colonization potential (Fernandez-Illescas *et al.* 2001), and the balanced competition model where the respective superior competitor becomes self-limiting (Scholes & Archer 1997; House *et al.* 2003). Competition-based approaches typically assume that the tree-grass competitive balance is independent of life-stage. However, there is evidence for the reverse, *i.e.* grasses reducing the emergence and survival of tree seedlings (Sankaran *et al.* 2004). Furthermore, resource-competition alone was not sufficient to produce long-term tree-grass coexistence in spatial simulation models (Jeltsch *et al.* 1996; Jeltsch *et al.* 1998a; Jeltsch *et al.* 2000). Therefore, demographic bottleneck models are currently favoured over competition-based approaches (Sankaran *et al.* 2004).

Demographic bottleneck models take life stages explicitly into account and focus on disturbances and climatic variability limiting tree recruitment and growth (Sankaran *et al.* 2004). In the savanna model of Jeltsch *et al.* (2000), disturbances such as fire, grazing or wood cutting act as buffers preventing savannas from deviations towards wooded systems or grasslands. Higgins *et al.* (2000) explain tree-grass coexistence with a storage effect: Tree recruitment is pulsed in time following stochastic rainfall patterns. The longevity of trees enables them to persist over periods with precipitation patterns that are sufficient only for grass reproduction and not for tree reproduction. There is agreement that in arid savannas, the primary demographic bottlenecks of woody species are germination and seedling establishment (Jeltsch *et al.* 1998a; Higgins *et al.* 2000; van Wijk & Bouten 2001). In demographic bottleneck models, the complementary problem to that of competition-based models arises, *i.e.*, that competition is either not included at all or modelled only semi-quantitatively (Sankaran *et al.* 2004).

Whether empirical evidence is supportive or not for a specific coexistence mechanism largely depends on the system investigated. Hence, a unifying mechanism explaining tree-grass coexistence is still lacking, but its characteristics can be formulated according to the existing empirical and theoretical evidence: It should incorporate characteristics of both competition-based and demographic bottleneck approaches (Sankaran *et al.* 2004). The competitive balance between trees and grasses should depend on life stage, as well as time and environmental gradients (Sankaran *et al.* 2004). Competitive exclusion can theoretically be

prevented by introducing life-stage-dependent covariance between environment and competition into savanna models, *i.e.*, strong intra-life form competition during favourable periods for that life form and strong inter-life form competition otherwise (Chesson *et al.* 2004). Thereby, the unifying mechanism would also integrate the majority of the other tree-grass coexistence mechanisms suggested thus far.

Patch dynamics has the potential to meet all these criteria of a unifying mechanism for the explanation of tree-grass coexistence in savannas. The patch-dynamics mechanism was first elaborated and applied to several different plant communities in a seminal paper by Watt (1947). A patch-dynamic system consists of a spatial mosaic of patches in which the same cyclical succession of patch states occurs. In different patches, the duration of successional states can vary and proceeds spatially asynchronously. At the landscape-scale, the proportions of the different patch states are stable giving the impression of a system at equilibrium. The landscape-scale coexistence of different communities representing the successional states depends on disturbances that prevent the persistence of a climax state (Pickett & White 1985) and on the possibility of reinvasion into early successional patch states from neighbouring patches. Promoting patch dynamics for the explanation of community patterns is a consequence of the insight that the integration of scale concepts into ecological study is of global concern (Levin 1992; Peterson & Parker 1998). Patterns observed at one scale are likely to be caused by mechanisms operating at other (mostly smaller) scales (Levin 1992), which is inherent in the patch-dynamics concept.

Patch-dynamics is related to the metapopulation concept (Levins 1969; Hanski 1994) where long-term persistence of a metapopulation is ensured by dispersal between patches in which local extinction may occur. While the metapopulation concept applies to populations of one species, patch-dynamics can explain the coexistence of many different species or life forms. In contrast to the metapopulation approach, the patch-dynamics concept specifies a particular within-patch community dynamic, *i.e.*, cyclical succession. In line with this, Levin et al.'s (2001) theoretical model of patch-dynamics is a hierarchical generalization of Levins' (1969) metapopulation model to more than one species. Apart from theoretical approaches, patch-dynamics have also been shown to be an appropriate description for several different communities, including heathland (Watt 1947), rocky intertidal communities (Levin & Paine 1974), forests (Remmert 1991), grasslands (Coffin & Lauenroth 1990), and plankton communities (Steele 1978).

First empirical studies suggest that patch-dynamics may also be applied to explain savanna dynamics (Gillson 2004; Wiegand *et al.* 2005; Wiegand *et al.* 2006). In light of the large temporal and spatial scales involved in a patch-dynamic landscape, simulation models are a suitable tool to comprehensively test the validity of the patch-dynamics approach and its implications for the explanation of tree-grass coexistence in savannas.

However, before patterns can be understood at large scales, mechanisms have to be investigated at the small scale (Wu & Loucks 1995). In a patch-dynamic system, cyclical succession is the process expected to occur at the small scale. In cyclical successions, different species or life forms replace each other in a predictable series from better colonizers to better competitors. The process is reset by the marked decline or extinction of the climax species, thereby closing the cycle. The cue triggering this decline can be inherent to the relationship between colonizers and competitors (Wiegand *et al.* 1998) or, more commonly, is a disturbance event that occurs with sufficiently high frequency to prevent a persistent climax stage. The occurrence of cyclical successions has been shown for a great range and diversity of plant and animal communities, for instance beech forests (Wissel 1992; Rademacher *et al.* 2004), small rodent communities (Erdakov *et al.* 1991), fire-driven plant communities (Larocque 2002), alpine cushion-tussock communities (Mark & Wilson 2005), coastal marsh vegetation (Miller *et al.* 2005), or the African tiger bush (Guillaume *et al.* 2001). If tree-grass coexistence in savannas can be explained with patch-dynamics, cyclical succession between grassy and woody dominance should occur at the patch-scale.

Hence, the overall objective of the present dissertation was to develop, implement, validate, and analyse a patch-scale simulation model of a semi-arid savanna to test whether cyclical succession can emerge from a realistic parameterization of the model.

If cyclical successions prevail in savannas, this also has implications for the management of shrub encroachment. In a patch-dynamic savanna, shrub encroachment is a natural, transient part of the successional cycle. This will pose new questions related to the relative importance of overgrazing and natural causes of shrub encroachment. Hence, it is essential to identify the drivers of cyclical successions and particularly of the phase dominated by woody plants. Fire, herbivory, and pulsed resources such as nutrients or water are potential candidates

for disturbance events driving successional cycles in arid ecosystems. Particularly the potential contribution of pulsed resources to cyclical successions in arid ecosystems is promising and has not yet been well studied (Chesson *et al.* 2004). This is also a reason why I conduct my investigations in a semi-arid savanna, because only for savannas receiving less than 650 mm of mean annual precipitation, recent comprehensive field evidence has shown a significant relationship between the pulsed resource precipitation and shrub cover (Sankaran *et al.* 2005).

Therefore, additional aims of this dissertation derived from the overall objective were

(1) to develop a conceptual mechanism underlying cyclical succession in savannas;

(2) to collect empirical and model-based evidence for this conceptual mechanism with particular reference to the temporal variation of the relative importance of competitive and facilitative tree-tree interactions;

(3) to determine the spatial and temporal resolution (*i.e.*, patch size and duration of cycles) of a patch-dynamic semi-arid savanna.

(4) to identify the drivers of cyclical successions with a focus on the investigation of fire and precipitation;

(5) to assess the relative importance of competition and demographic bottlenecks for tree-grass coexistence in savannas;

(6) to discuss the management implications of shrub encroachment as a natural phase in cyclical successions of savanna communities.

In order to achieve these aims, I collected data at a semi-arid savanna site in South Africa and developed the spatially explicit, individual-based, patch-scale simulation model SATCHMO (**SA**vanna pa**TCH MO**del). The field data were used for several purposes:

- to assemble the empirical evidence for the cyclical succession mechanism with respect to competition and facilitation with spatial pattern analyses and an experimental approach (Chapter 2),
- to investigate the importance of fire for shrub population dynamics based on morphometric analyses (Chapter 3),
- to determine patch size which required the development of a new technique (Chapter 4), and
- to achieve a realistic parameterization and validation of SATCHMO (Chapter 5).

A sensitivity analysis of SATCHMO was conducted to identify the relative importance of fire, soil moisture, and demographic parameters for shrub cover and population size dynamics (Chapter 5). Finally, age- and size-frequency distributions and shrub cover time series generated with SATCHMO were analysed to provide support for the conceptual mechanism underlying cyclical succession and to establish the role of precipitation as a driver of cyclical succession (Chapter 6).

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2

Multi-proxy evidence for competition between savanna woody species

Meyer K.M., Ward D., Wiegand K., Moustakas A. (in prep.) *Plant Ecology*.

Abstract

Factors affecting the coexistence of trees and grasses in savannas are not yet agreed upon but coexistence should be possible if competition between the woody and the grassy components is less intense than the competition within each component. Although several studies have investigated competition between trees and grasses, little is known about tree-tree-interactions. We used a multi-proxy approach to examine the spatial pattern of *Acacia mellifera* and other savanna woody species in a semi-arid savanna in South Africa. Spatial analysis of the point patterns of young and reproductively mature shrubs detected decreasing aggregation with size/age over all spatial scales. This indicated the prevalence of competition although the overall spatial shrub pattern was aggregated. In contrast to point pattern statistics that detect changes only when competition has led to the death of the inferior competitor, we also applied methods identifying the competitive effect on size. Competition should lead to a negative spatial autocorrelation in size, which we observed in half of the studied cases. Quantile regressions show that nearest neighbour distance increased steeply with combined size of the target shrub and its neighbours indicating strong competitive effects. The medians of the distributions of maximum root lengths of *A. mellifera*, of the scale of regular patterns, and of negative autocorrelations were not significantly different, suggesting that overlapping root systems mediate competitive interactions. A competitor removal experiment did not lead to increased shrub sizes which may be due to the limited duration of the experiment. From the nearest-neighbour and autocorrelation analyses, we conclude that competition had a strong impact on growth rates of savanna woody species. Competition-induced mortality only becomes obvious when analysing the shift towards less aggregated spatial patterns when shrubs become reproductively mature. As the overall clustered spatial pattern masks the perceptible effect of competition, a time-component should always be included in spatial pattern-based inference of competition.

Key Words

Acacia mellifera, competitor removal experiment, nearest neighbour distance, quantile regression, spatial autocorrelation, spatial point pattern analysis.

Introduction

Clements *et al.* (1929) postulated that the composition of any mature stand of vegetation is shaped by competition (see also Wilson & Tilman 1991; Silvertown 2004). Theoretically, coexistence of life forms within a mature stand of vegetation is possible if competition within life forms is stronger than competition between life forms (Scholes & Archer 1997). Through time, a multitude of approaches has been developed to infer competition from physiological and morphometric relationships, and, more recently, from spatial patterns (*e.g.*, Clements *et al.* 1929; Pielou 1962; Welden & Slauson 1986; Shackleton 2002; Wiegand & Moloney 2004). However, there have been only few attempts to apply different approaches to data from the same study area to compare results from inferential and experimental methods (*e.g.*, Goldberg *et al.* 1999; Freckleton & Watkinson 2000; Kint *et al.* 2003). Savannas constitute classic examples of a vegetation type maintained through the coexistence of two dominant life forms, namely woody species and grasses. Thus far, the relationship between these life forms has been more often in the focus of savanna research than intra-life form interactions (*e.g.*, Brown *et al.* 1998; Fetene 2003). Little emphasis has been placed on positive and negative interactions among trees in determining their spatial pattern and density despite the fact that tree density defines savannas as open or closed (Couteron & Kokou 1997; Scholes & Archer 1997). Facilitation is a positive interaction leading to the aggregation of plants, thereby increasing densities (Scholes & Archer 1997; Bruno *et al.* 2003). Worldwide, increasing densities of woody species often unpalatable to livestock pose growing ecological and economic problems to tree-grass coexistence in savannas. This intensifying shrub encroachment supports the assumption that aggregated spatial patterns of woody species prevail in many savannas and are maintained by facilitative interactions or other mechanisms causing aggregation. On the other hand, competition among trees may limit the density and spatial pattern of trees to the extent that savannas do not become woodlands (Jeltsch *et al.* 2000). This is particularly true for savannas with a mean annual precipitation of less than 650 mm where maximum woody cover is increasing with increasing mean annual precipitation (Sankaran *et al.* 2005)

indicating the prevalence of competition for soil moisture. Hence, tree-tree competition may be an important driving factor in maintaining the existence of the savanna biome.

In the light of increasing aggregation of woody species in savannas, the identification of parallel competitive interactions is a growing challenge for the methodological tool set of a spatial ecologist. In general, the use of spatial methods is favoured over non-spatial methods because they retain more information. Spatial pattern analysis is an indirect approach to evaluating interaction among plants (Couteron & Kokou 1997) without the need for costly long-term demographic censuses. A shift towards less aggregated distributions of plants indicates density-dependent mortality, possibly caused by intra-specific competition for an evenly-distributed resource (Wolf 2005). Aggregation can result from vegetative reproduction, clumped seed dispersal, heterogeneity of soil resources, temporary local release from recruitment limitation, disturbances, facilitation, or a combination of these factors (Ford 1975; Phillips & MacMahon 1981; Skarpe 1991). Plants are randomly spaced either due to the absence of processes causing regularity or aggregation or because processes causing regularity and aggregation are balancing each other, *e.g.*, in a transient state between aggregation and regular distribution (Skarpe 1991). Competition also leads to a negative spatial autocorrelation in plant size, so that taller plants have smaller neighbours (Cannell *et al.* 1984; Purves & Law 2002). Spatial point pattern statistics can be used to identify at which scales a spatial pattern is significantly clustered or regular and at which scales individual size-measures are spatially autocorrelated. Point pattern statistics incorporate more information from a fully mapped spatial pattern than most other spatial methods.

However, if the aim is to differentiate between intensity and importance of competition, nearest-neighbour analysis is the method of choice (Welden & Slauson 1986). As competition may control the size and density of savanna trees (Smith & Walker 1983), competition has also been inferred by nearest neighbour analysis of *Acacia* stands (Gutierrez & Fuentes 1979; Smith & Goodman 1986; Benshahar 1991). The combined size of a plant and its nearest neighbour is generally positively correlated with the distance between them (Gutierrez & Fuentes 1979; Smith & Walker 1983). Nearest neighbour analysis has been criticised to underestimate the prevalence of competition because the nearest neighbour may not have the greatest competitive impact on a target plant if the nearest neighbour is very small compared to other plants in the vicinity (Shackleton 2002). This limitation can be

overcome by using more than one nearest neighbour (Shackleton 2002). It is a simple and rapid method which can be very insightful in combination with other methods such as the scale-dependent spatial point pattern analysis used here (see application in, *e.g.*, Grundy *et al.* 1994 (three nearest neighbours); Shackleton 2002; Ward 2005). Spatial point pattern analysis is particularly effective when the effects of competition are sufficiently strong to result in differential mortality, whereas nearest-neighbour analysis may also detect weaker competitive effects among living individuals.

While inference of competition from spatial patterns is indirect, experimental competitor removal is a direct method and should be preferred when the focus lies on the isolation of the effects of competition. The disadvantage of experimental approaches is that it may be much more time-consuming than spatial pattern analysis.

The aim of the present study is to investigate whether the prevalence of competition among *Acacia mellifera* (Vahl) Benth. and other woody components of a semi-arid savanna in South Africa can be inferred with different spatial pattern analysis methods and an experimental approach in the presence of spatial aggregation and time-constraints. We do not separate inter-shrub competition further into intra- and inter-specific competition because we assume that interactions at the species level are of minor importance for the understanding of savanna dynamics. If we assume that inter-shrub competition is the major driver in the shrub community investigated, we can derive the following predictions:

1. Spatial point patterns of young and old woody species will show less aggregation with age.
2. There will be a negative spatial autocorrelation in shrub sizes.
3. The combined size of four neighbours will increase with the sum of the distances to the four nearest neighbours.
4. Competitor removal will lead to increases in shrub size.

Methods

Study area

The study was conducted in semi-arid savanna in the Kalahari thornveld at Pniel Estates (S 28° 35', E 24° 29'), 30 km north of Kimberley, South Africa, in January and February 2004 and in January 2005. Mean annual precipitation is 377 mm and mostly occurs as thunderstorms throughout the summer months (September to

March). *A. mellifera* is the dominant plant species in the study area; *Tarchonanthus camphoratus* and *A. tortilis* are the other important woody species.

Field methods

To explore the spatial pattern of the woody species in the study area, we set up 20 fenced 15 m × 15 m plots. Within the plots, we determined the *x*- and *y*-coordinates and the maximum canopy diameter of all *A. mellifera* (n = 880), *A. tortilis* (n = 89), and *T. camphoratus* (n = 108) individuals (total n = 1077 shrubs, minimum n = 10 shrubs/plot, maximum n = 167 shrubs/plot). There were no other woody species present in the plots.

To investigate the effect of competitive release on shrub growth, we set up a competitor removal experiment. All aboveground parts of all woody species within a radius of 7.5 m around 15 *A. mellifera* "target" shrubs were cut and poisoned in February 2004. In the vicinity of each target shrub, a control shrub was marked. The maximum canopy diameter, the canopy diameter perpendicular to the maximum canopy diameter, and three shrub heights were determined for every target and control shrub directly before the poisoning and 11 months later.

In a set of ten 10 m x 10 m plots, we determined the length of the regrowth of the present season at the tips of up to 10 branches per *A. mellifera* shrub in 2004 (n = 309 shrubs) and 2005 (n = 281 shrubs). To determine the adult mortality rate, we counted the number of *A. mellifera* shrubs that died between 2004 and 2005 in these plots.

We excavated 16 lateral roots of 10 *A. mellifera* shrubs and determined their maximum lengths. We restricted the excavations to the shallow lateral roots due to logistic constraints and because the small taproot of *A. mellifera* is of minor importance for water and nutrient uptake compared to the lateral roots in *A. mellifera*.

Spatial pattern analyses

We analysed the spatial distribution of woody individuals in the 20 15 m × 15 m plots in two approaches, the "split approach" and the "overall approach": We split the *A. mellifera* shrubs in the 20 15 m × 15 m plots into those with a canopy diameter of less than 145 cm ("small") and those with a greater canopy diameter ("large") to test the hypothesis that originally aggregated shrub seedling patterns become less aggregated with individual life time due to the action of competition (split approach). A canopy diameter of 145 cm represents the threshold for seed

production and therefore reproductive maturity in *A. mellifera* (D. Ward, unpublished data). As a rule of thumb, a pattern to be analysed with spatial point pattern statistics should comprise at least about 30 points (T. Wiegand, pers. comm.), which was fulfilled by only 12 plots in the split approach. Therefore, we also analysed the spatial distribution of all individuals of all shrub species occurring in all 20 15 m × 15 m plots to be able to compare it with the size-dependent *A. mellifera* patterns (overall approach).

In both approaches, we applied the univariate Wiegand-Moloney *O*-ring statistic with the null-hypothesis of complete spatial randomness (CSR, Wiegand & Moloney 2004). The Wiegand-Moloney *O*-ring statistic is used to analyse the second order properties of fully-mapped spatial point patterns and is similar to Ripley's *K* statistic (Ripley 1976; Besag 1977; Ripley 1981). In contrast to Ripley's *K*, the *O*-ring function measures interaction at distance *h* only, without a memory effect from integration over all distances up to *h* (Wiegand & Moloney 2004, for a description of the statistic, see Appendix). Wiegand-Moloney's *O*-ring function is equal to Stoyan and Stoyan's pair-correlation function (Stoyan & Stoyan 1994) multiplied with the intensity of the pattern λ. Upper and lower confidence envelopes were generated from 99 simulations resulting in a confidence level of $p = 0.01$. The point pattern analyses were carried out with the *Programita* software (Wiegand & Moloney 2004) which also offers a function to combine replicates to obtain a generalization of the spatial patterns in a study area. Hence, we analysed the 12 replicates of the small shrub-patterns combined (split approach), the 12 replicates of the large shrub-patterns combined (split approach), and the 20 replicates of the overall approach combined. In the overall approach, we also determined the frequency distribution of significantly regular patterns at scales from 0 to 500 cm over all plots separately with a grid cell size of 10 cm.

Spatial autocorrelation

To examine the average similarity or dissimilarity in size of neighbouring shrubs, we investigated the spatial autocorrelation of the shrub canopy diameters at different spatial scales *h* in the 15 m × 15 m plots by calculating Pearson's correlation coefficient between the canopy diameter at point *i* and the mean of the canopy diameters of points within a ring centered on *i* with radius *h* and width δh. The frequency distribution of negative autocorrelation at scales from 0 to 590 cm was determined over all plots separately. The autocorrelation analyses were carried out with the *Programita* software (Wiegand & Moloney 2004).

Nearest neighbour analyses

For all shrubs in the 15 m × 15 m plots, we investigated the relationship between the sum of the distances to the four nearest neighbours and the sum of the canopy diameters of the target shrub and its four nearest neighbours. As variance was not homogeneous across the range of ***x***-values, we used quantile regression instead of conventional linear regression (Goldberg & Scheiner 1993; Thomson *et al.* 1996). In quantile regression, different parts of the variance are captured by different quantiles (Koenker & Bassett 1978). Quantile regression functions are estimated as the minimized asymmetrically-weighted sum of absolute residual errors (Koenker & Bassett 1978; Cade *et al.* 1999; Cade 2003)). The τ^{th} quantile regression function, $Q(\tau)$, describes a linear or nonlinear fit through the data so that τ proportion of the data is less than $Q(\tau)$ and 1- τ proportion is greater than $Q(\tau)$. The upper quantile is a more appropriate representation of the limiting factor than the central estimate of a conventional regression (Thomson *et al.* 1996). The greater the similarity in slope of the upper quantiles, the smaller is the proportion of the sample that is affected by the interaction with unmeasured factors (see also Meyer *et al.* 2005). Nearest neighbour and quantile regression analyses were carried out with the software package S-PLUS 6.1.

Morphometric analyses

In the competitor removal experiment, the relative growth rates

RGR = ln(final size/initial size) /(final time step-initial time step)

(Larcher 2003)

of height and canopy diameter of control and target shrubs were compared using *t*-tests with Welch's correction for unequal variances.

Results

In the split approach, the spatial pattern of the small shrubs in the 12 combined 15 m × 15 m plots was significantly clustered relative to the null model of complete spatial randomness at virtually all scales up to 500 cm ($p < 0.01$, Fig. 2.1a). Contrarily, the spatial pattern of large shrubs in the 12 combined 15 m × 15 m plots of the split approach was random at virtually all scales with a significant deviation to regularity at 350 cm ($p < 0.01$, Fig. 2.1b). In the overall approach, the combined analysis of all shrubs in the 20 15 m × 15 m plots produced equivalent results to the small shrub pattern analysis: significant aggregation at virtually all scales ($p < 0.01$).

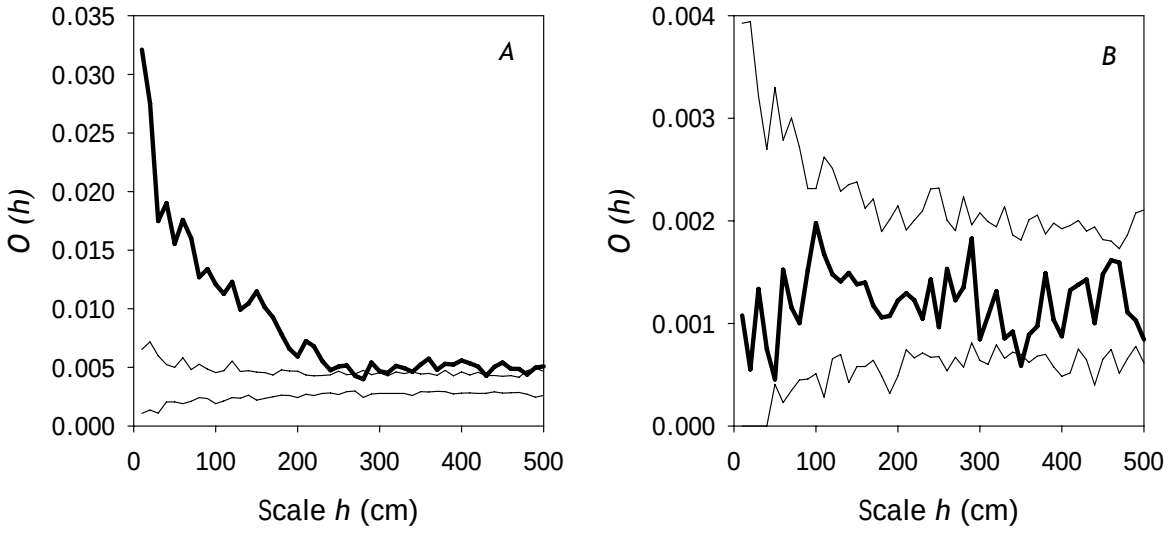

Fig. 2.1: The univariate *O*-ring statistic *O*(*h*) at different scales *h* (bold lines) with upper and lower confidence envelopes (thin lines) representing the maximum and the minimum value from 99 simulations with the null-hypothesis of complete spatial randomness combined for small (*A*) and large (*B*) *A. mellifera* shrubs in 12 15 m × 15 m plots (split approach). The threshold separating small and large shrubs was a canopy diameter of 145 cm which is the size at reproductive maturity. If *O*(*h*) is above the upper confidence interval, the pattern is significantly clustered, if *O*(*h*) is below the lower confidence interval, the pattern is significantly regular at the considered scale ($p < 0.01$).

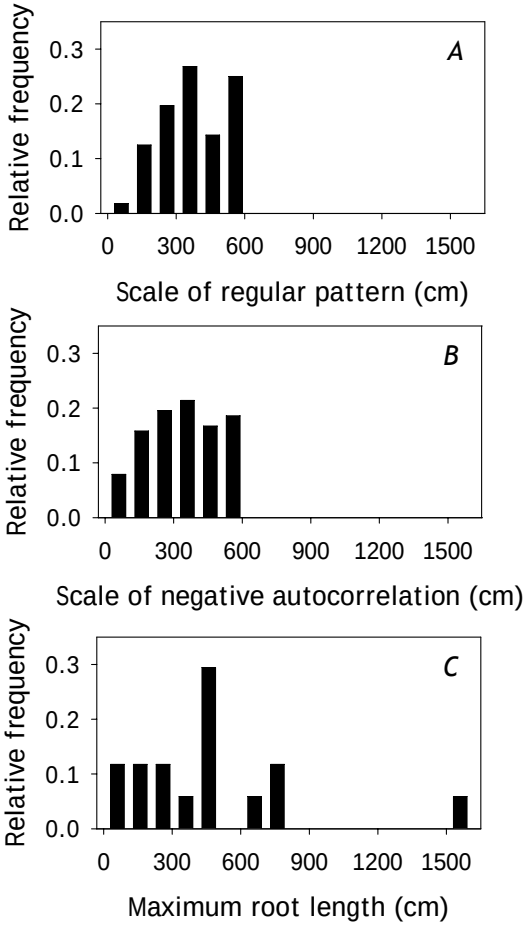

Fig. 2.2: Relative frequency distributions of (*A*) regular patterns at different scales, (B) negative autocorrelation at different scales, and (*C*) of the maximum root length. (*A*) Point pattern analysis was carried out for all woody plants in 20 15 m × 15 m plots at scales from 0 to 590 cm on a plot basis with the null model of complete spatial randomness (overall approach). Only the relative frequencies of the significantly regular patterns over all plots are presented. (*B*) Autocorrelation analysis of the canopy diameter of all woody species in 20 15 m × 15 m plots was performed at scales from 0 to 590 cm with Pearson's correlation index. Only the relative frequencies of the significantly negative autocorrelations over all plots are presented. *(C*) Maximum root length was determined for 16 roots of 10 *A. mellifera* shrubs.

When the plots of the overall approach were analysed separately, the rare occurrence of a significant regular pattern was most probable at scales around 330 cm (= mode in Fig. 2.2*a*). In the 15 m x 15 m plots, negative spatial autocorrelation in the canopy diameter of all woody species occurred approximately as often as positive autocorrelation (see Table 2.1 for mean canopy diameters). We obtained non-significant autocorrelation results in a few cases only. The mode of the frequency distribution of the scales at which negative autocorrelation occurred was 370 cm (Fig. 2.2*b*).

Table 2.1: Mean and standard deviation (S.D.) of parameters estimated from the competitor removal experiment, the 15 m × 15 m plots, and the 10 m × 10 m plots. In the competitor removal experiment, relative growth rate (RGR) was investigated for control shrubs and target shrubs, whose woody competitors where removed within a radius of 7.5 m over a one-year period. No treatments were applied to the 10 m × 10 m plots and the 15 m × 15 m plots. All parameter units are cm, except year^{-1} for adult mortality and RGR which is dimensionless. *n* = sample size, *A. mellifera* = *Acacia mellifera*, *T. camphoratus* = *Tarchonanthus camphoratus*.

Species	*n*	Parameter	Mean	S.D.
Competitor removal experiment				
A. mellifera	15	RGR in target height	0.06	0.10
A. mellifera	15	RGR in control height	0.05	0.05
A. mellifera	15	RGR in target canopy diameter	0.07	0.11
A. mellifera	15	RGR in control canopy diameter	0.02	0.10
15 m x 15 m plots				
A. mellifera	880	Canopy diameter	112.79	104.73
A. tortilis	89	Canopy diameter	79.88	67.16
T. camphorates	108	Canopy diameter	119.72	81.97
10 m x 10 m plots				
A. mellifera	309	Annual regrowth length	3.38	3.43
A. mellifera	309	Adult mortality	0.0065	0.0803

There was a significantly positive relationship between combined nearest neighbour distance and combined canopy diameters in the 15 m x 15 m plots (Fig. 2.3*a*) because the lower 90% confidence intervals of the slopes of all quantile regression lines were greater than 0 (Fig. 2.3*b*). The 0.999-quantile had a very steep slope (slope = 1.51, Fig. 2.3*b*), corresponding with a high intensity of competition (*cf.* Welden & Slauson 1986). Because the quantiles did not have similar slopes (Fig. 2.3*b*), unmeasured factors played an important interactive role

in the relationship between combined canopy diameters and nearest neighbour distances.

Relative growth rates in height (t = -0.80, df = 42.77, p = 0.43) and canopy diameter (t = -1.72, df = 54.97, p = 0.09) were not significantly different for control and target *A. mellifera* shrubs in the competitor removal experiment (Table 2.1). Total rainfall between poisoning and data collection (230 mm) was lower than the long-term mean for those 11 months of the year (320 mm, Zucchini & Adamson 1984).

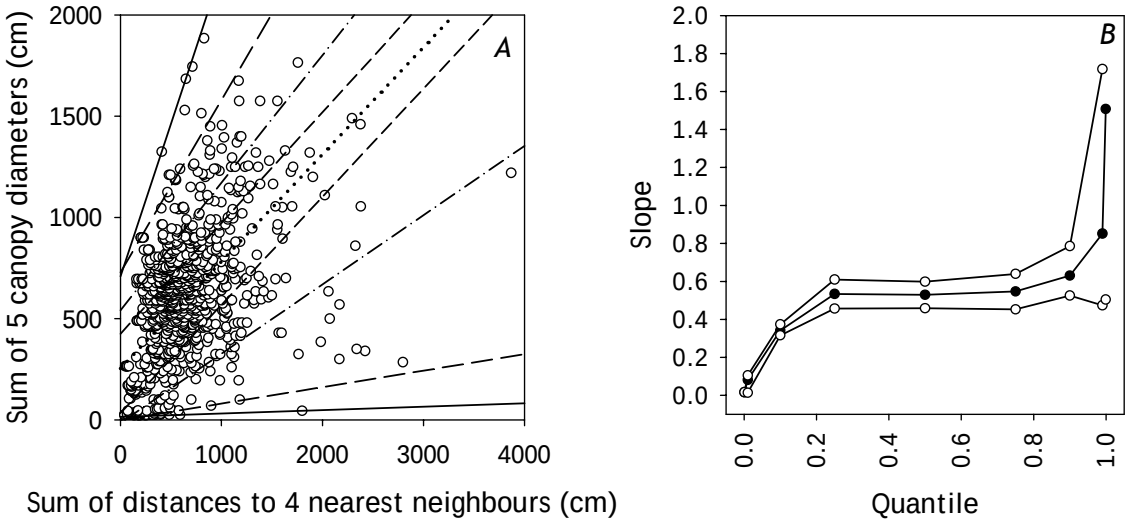

Fig. 2.3: Relationship between the sum of the canopy diameters of the target shrub and its 4 nearest neighbours and the sum of the distances to the 4 nearest neighbours in the 15 m × 15 m plots (n = 1077). The plots consisted of the shrub species *A. mellifera*, *A. tortilis*, and *T. camphoratus*. (*A*) Quantile regression estimates. Quantiles from top to bottom: solid line: 0.999-quantile, long-dashed: 0.99-quantile, dot-dashed: 0.9-quantile, short-dashed: 0.75-quantile, dotted: 0.5-quantile, short-dashed: 0.25-quantile, dot-dashed: 0.1-quantile, long-dashed: 0.01-quantile, solid line: 0.001-quantile. (*B*) Slopes of the quantile regression lines in (*A*) (solid circles) with upper and lower 90% confidence intervals (open circles).

Over the two study years, *A. mellifera* showed an annual growth rate of 2.63 cm/year (Table 2.1). From 2004 to 2005, two out of 309 *A. mellifera* shrubs died in the 10 m x 10 m plots, giving an annual adult mortality rate of 0.0065 (Table 2.1).

The location of the frequency distribution of maximum root lengths (Fig. 2.2*c*) was not significantly different from the frequency distributions of the scale of regular patterns (Fig. 2.2*a*) and of autocorrelation (Fig. 2.2*b*) in the 15 m x 15 m plots (p = 0.50 and p = 0.24, respectively) although the power of these tests was very low (1-β <0.03).

Discussion

Spatial point pattern analysis showed that the overall spatial pattern of woody species in the study area was clustered. However, the separate analysis of small and large shrubs revealed that this was due to the strong aggregation of small plants that had not reached reproductive maturity. The spatial pattern of the reproductively mature *A. mellifera* shrubs was random at all scales except 350 cm where it was significantly regular. Age and size do not have to be related in savanna shrubs but in *A. mellifera*, height and shape have been shown to be reliable indicators of age (Adams 1967). It follows that over the life-time of an individual, patterns become less aggregated in the study area which provides evidence for competitive interactions in the individuals' past. Hence, we can corroborate prediction 1. However, the competitive effect is masked by the overall aggregation of shrubs. Several earlier studies also reported clustered or random distributions for *Acacia* and other savanna woody species (Skarpe 1991; Couteron & Kokou 1997; Barot *et al.* 1999; Wiegand *et al.* 2000a). This underlines the importance of explicit consideration of time when inferring processes from spatial patterns. Only when time is included, prevailing competitive effects can be distinguished from a possibly much stronger effect of aggregation early in the life-time of individuals (Wolf 2005; Getzin *et al.* accepted). If chronosequences are not available, the age of plants or proxies for the age (as in this study) can be used to include a time-component into the analysis.

The distinct aggregation that we found for young woody savanna species may have many reasons. Although vegetative reproduction is often considered to be the proximate mechanism that leads to aggregation in woody species (Phillips & MacMahon 1981), we did not find any evidence for vegetative reproduction in *A. mellifera* during the root system excavations of the present study. Scholes and Archer (1997) suggest topography (*e.g.*, termite mounds), soil depth, and fire patchiness as potential factors that may generate aggregated spatial patterns in savanna plants. In the study area, topography is relatively homogenous, few termite mounds were observed, soil depth was similar in all plots, and fuel loads are too low to support many fires. Nevertheless, fire has been suggested to cause clustered growth patterns of *A. mellifera* by preventing field layer vegetation from entering the *A. mellifera* thickets (Skarpe 1991). However, it is more probable that aggregated seed dispersal caused the observed patterns of small shrubs. At the study site, field observations indicate that seedling density declines almost exponentially with distance from the rooting point of the parent shrub (K. Meyer,

unpublished observations of two reproducing shrubs). This aggregated dispersal could be enhanced by a facilitative effect of the parent shrub or other large shrubs in the vicinity. In facilitative interactions, "nurse plants" create nutrient and soil moisture-rich patches under their canopy promoting germination and establishment of other (mostly smaller) plants (Belsky 1994; Holzapfel & Mahall 1999; Münzbergova & Ward 2002). This can lead to a temporary local release from recruitment limitation during periods of favourable environmental conditions, *e.g.*, overlapping local rainfall events. A combination of facilitation and aggregated seed dispersal is also consistent with the observation of less aggregated larger shrubs that may act as nurse plants for their own clustered progeny.

However, also in the overall approach, regular spatial patterns were detected in some cases. Additionally, negative autocorrelation in canopy diameter was observed in half of the cases indicating competitive action in the past (Prediction 2). Here, competition may act in a way that competitively-superior trees impair the viability or the growth of their neighbours. This was supported by the fact that the most frequent scale of regular patterns and of negative autocorrelation matched the average maximum root length. Maximum root length can be taken as a simple surrogate for the maximum extension of the zone of influence of a plant (Casper *et al.* 2003). Two plants compete with each other when their zones of influence overlap. The greater the overlap, the more intense is the competition. Hence, in our case, the regular pattern and negative autocorrelation may result from zones of influence whose maximum degree of overlap is restricted by the intensity of competition: As soon as the edge of a zone of influence of one plant reaches the centre of the zone of influence of another plant, the competitively-inferior plant dies (regular pattern) or at least grows less in diameter (negative autocorrelation). Those cases where we did not find regular spatial patterns or negative autocorrelation can be attributed to the early phase in the transition from an originally clustered pattern via a random to a regular pattern. This indicates that small aggregated plants are present at greater densities in the study area than large plants that have survived the increased competitive pressure at greater individual shrub sizes.

Supporting prediction 3, the results from the nearest neighbour analyses are consistent with several studies inferring the existence of competition in *Acacia* species (Gutierrez & Fuentes 1979; Smith & Walker 1983; Smith & Goodman 1986). Wiegand *et al.* (2005) have shown that inter-trees distances increase with age/size and Ward (2005) has shown that trees become more evenly spaced with age/size.

For the study area, the nearest neighbour analyses did not only show the existence of competition but also the high intensity thereof (inferred from the steep slope of the upper limiting quantile in Fig. 2.3a; Welden & Slauson 1986). Nevertheless, our analyses also support the hypothesis of Welden & Slauson (1986) that the intensity of competition and its importance relative to other factors are independent of each other: The similar slopes of the quantile regression lines (Fig. 2.3*a*) lead to the conclusion that unmeasured factors other than nearest neighbour distance also had an important (interactive) effect on shrub size. These other factors could be, for instance, nutrient heterogeneities or water stress. This result may enhance the view that, in arid savannas, aboveground competition for light (as revealed by nearest-neighbour analyses) is of minor importance compared to belowground competition for water and nutrients (Vila 1997). However, only long-term studies can generate reliable conclusions on the relationship between growth and space (*cf.* Wiegand *et al.* 2000b).

The experimental removal of competitors did not have a significant positive effect on shrub size, which is inconsistent with prediction 4. This is even more surprising as shrub removal is expected to have a fertilizing effect on target shrubs through the decomposition of the roots of the removed competitors. However, some of the "removed competitors" were able to produce viable regrowth in spite of having been poisoned. Hence, viability and especially belowground competitive strength may not have been completely impaired by the poisoning treatment. Rainfall was below the long-term average in the period between competitor removal and data collection. This may be the reason for the generally low growth rates of *A. mellifera* observed in this study. Growth may have been too slow to cause a significant difference in relative growth rates of targets and controls (see also Wiegand *et al.* 2005). In general, demographic processes were very slow in *A. mellifera* because mortality and growth rates were very low in the study period; we found only two dead trees and a growth rate of annual regrowth at the tips of the branches of 3.4 cm/year.

Overall, the existence of competition in the study area was inferred by spatial point pattern analysis and autocorrelation analysis, as well as nearest neighbour analysis (with high intensity). The competitor removal experiment did not support an explanation involving competition but this may be due to an insufficient duration of the treatments.

Although an experimental approach may be more powerful in general, we showed that if demographic processes are slow - as it is commonly the case in arid

areas – inferential methods such as spatial point pattern statistics or nearest neighbour analyses are more time efficient and still provide similarly satisfying answers compared with experiments. In spatial analyses, it is important to include a time-related component that allows inference of competition if patterns become less aggregated over time. From the spatial analyses, we conclude that competition acts after the onset of individual reproductive maturity turning the originally aggregated shrub pattern into a less aggregated pattern. Only then, the overlap of root systems may be strong enough to lead to perceptible changes in growth and spatial patterns of savanna woody species that can be detected in spite of overall aggregated spatial patterns.

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Appendix

The basic idea behind Wiegand-Moloney's *O* is to construct concentric rings with radius *h* and width *δh* around each point in the study area, to count the number of points within these rings, to take the average across all rings of the same radius, and to compare it to the number of points expected at scale *h* assuming a random process (Wiegand & Moloney 2004). The *O*-ring function is given as

$$O(h) = \frac{\frac{1}{N}\sum_{i=1}^{N} p_i(h,\delta h)}{\frac{1}{N}\sum_{i=1}^{N} area_i}$$

where *h* is the radius of the ring, *N* the number of points in the study area, *pi(h,δh)* the number of points within the ring of radius *h* and width *δh* around the point *i*, and $area_i$ is the area of the ring around point *i*.

3

Big is not better:

Small *Acacia mellifera* shrubs are more vital after fire

Meyer K.M., Ward D., Moustakas A., Wiegand K. (2005) *African Journal of Ecology 43*:131.

Abstract

Fire and acacias are vital components in savanna dynamics but little is known about the relationship between post-fire mortality and size of *Acacia* species. We determined mortality, height, and height of resprouts of the encroaching shrub species *Acacia mellifera* in a semi-arid South African savanna two years after fire. As expected, resprouting ability after topkill was high, only 9% of the studied shrubs died completely. Surprisingly, shrubs that died in the fire were significantly taller than their resprouting conspecifics. Results from quantile regression show that the height of regrowth relative to the total height of taller shrubs is less than in smaller shrubs, despite taller shrubs having more access to below-ground resources. We offer two possible explanations for these unexpected results: In taller shrubs, the maximum longitudinal growth rate of resprouts may be reached and therefore, resources may be invested in a greater number of resprouts or stored as reserves. Alternatively, resprouting ability may be impaired in old age by a senescence effect caused by the accumulation of physiological dysfunctions.

Key Words

size, flame zone, roots, below-ground traits, Kalahari thornveld, limiting factors.

Introduction

Although fire and acacias are vital components in African savanna dynamics, little is known about the impact of fire on *Acacia* life cycles (Midgeley & Bond 2001). Midgeley and Bond (2001) express the need for more research relating fire-sensitivity to size and age of *Acacia* species. In savanna woody species, topkill is much more frequent than complete mortality after fire (Hoffmann & Solbrig 2003). Rather, fire stimulates resprouting from below-ground tissues (Pendergrass *et al.* 1998). Studies on the relationship between shrub size and resprouting ability have not generated consistent results: the relationship is negative for woody species in wet prairies (Pendergrass *et al.* 1998), not significantly different from zero for a fynbos conifer (Keeley *et al.* 1999), and positive for several shrubs including *Acacia* species (Hodgkinson 1998), a *Prosopis* species (Wright *et al.* 1976), a mediterranean tree (Pausas 1997), and a *Pinus* species (Thanos *et al.* 1996). In temperate woodlands in Australia, resprouting ability is highest in medium size classes (Hodgkinson 1998). In general, tall trees are only severely damaged by fires of higher intensity (Morrison & Renwick 2000), as most parts of their canopy are above the flame zone of small to medium intensity fires.

Little is known about the relationship between total shrub height and height of regrowth after fire. Assuming a positive correlation between above- and below-ground size, taller plants should have more reserves that they can allocate to regrowth after fire, *e.g.*, in *Eucalyptus*, the growth rate of resprouts increases with pre-fire height (Hodgkinson 1992). Below-ground reserves are especially important for resprouting ability after fire (McGee *et al.* 1995). We expect that the height of regrowth should be proportional to the height of the shrub with a factor of at least 1.00.

A. mellifera Benth. is a resprouting multi-stemmed shrub with an average height of 75 cm (Meyer *et al.*, unpublished data) and frequently encroaches into open savannas, *i.e.*, densities of these plants can locally be so high as to convert an open (grass-dominated) savanna into a closed savanna or woodland (Smit 2004). Skarpe (1991) attributes the great fire susceptibility of *A. mellifera* to its small size, which constrains at least parts of its canopy permanently to the flame zone of grass fires. However, this relationship has not been studied in detail for *A. mellifera*. The present study investigates post-fire mortality and resprouting as a function of *A. mellifera* size and below-ground morphometrical traits.

Methods

Study area

The study was conducted in semi-arid savanna in the Kalahari thornveld at Pniel Estates (S 28° 35', E 24° 29'), 30 km north of Kimberley, South Africa, in January 2004. Mean annual precipitation is 388 mm and occurs as thunderstorms throughout the summer months (September to March). Blackthorn (*A. mellifera*), camphor tree (*Tarchonanthus camphorates*), and umbrella thorn (*A. tortilis*) were the dominant plant species on the shallow sandy soils of the study area. In November 2002, a fire of an estimated medium to high intensity affected the study area for 10 to 12 h until it was extinguished by the farm management.

Field methods

All *A. mellifera* shrubs were recorded along a 1500 m – long and 20 m – wide transect and were classified as dead and alive to determine post-fire mortality. A shrub was counted as dead if no regrowth could be identified and as alive if resprouts were present. We assumed that, with a time-lag of more than one year after a fire, a living shrub that lost all photosynthetic structures to the fire should have produced regrowth to survive. Therefore, we did not look for other live tissue than the clearly visible regrowth at the stem bases. The maximum height of the residual branches of all dead shrubs was determined to investigate the relationship between size and mortality. The maximum height of 30 randomly-chosen live *A. mellifera* shrubs and the height of their regrowth were determined. We assumed that the probability of an underestimation of maximum shrub height due to burnt-off branches was constant for all shrubs in the study area. In an adjacent part of the study area that was not affected by the fire, an index of below-ground growth was determined by measuring the length of subsurface roots within a randomly-chosen 60°-angle centered at the tap root from 16 *A. mellifera* shrubs. The entire lengths of these roots were excavated until they turned vertically downwards (to a depth of > 1m). The height of the shrubs and the length of the longest root (between tap root and the point of turning vertically downwards) were determined to explore the relationship between above- and below-ground morphometrical traits.

Data analyses

The heights of dead and live *A. mellifera* shrubs were compared with Wilcoxon's signed rank test. The relationships between height of regrowth and total height of

A. mellifera and between height and length of longest root were explored in quantile regressions because the data points assumed a triangular shape, suggesting an upper limiting factor and the impact of other unmeasured factors (*cf.* Goldberg & Scheiner 1993). Conventional linear regression assumes homogeneity of variance across the range of x-values (Sokal & Rohlf 1998). As this assumption was violated we used quantile regression (Goldberg & Scheiner 1993; Thomson *et al.* 1996). In quantile regression, different parts of the variation in the data are captured by different quantiles (Koenker & Bassett 1978). Quantile regression functions are estimated by minimizing an asymmetrically-weighted sum of absolute residual errors (Koenker & Bassett 1978; Cade *et al.* 1999; Cade 2003). The τ^{th} quantile regression function, $Q(\tau)$, describes a linear or nonlinear fit through the data so that τ proportion of the data is less than $Q(\tau)$ and 1- τ proportion is greater than $Q(\tau)$. The upper quantile is a more appropriate representation of the limiting factor than the central estimate of a conventional regression (Cade *et al.* 1999). The more that upper quantiles have the same slope, the smaller the proportion of the sample that is affected by the interaction with unmeasured factors (Cade 2003). The more that quantiles have the same slope, the more the impact of the unmeasured factors tends to be additive rather than interactive (Cade 2003). The software package S-PLUS 6.1 was used for statistical analyses.

Results

The mortality of *A. mellifera* was 0.09 in the study area (n = 747 shrubs), *i.e.*, 91% of the shrubs showed regrowth 14 months after a fire. Dead *A. mellifera* shrubs were significantly taller than live *A. mellifera* ($p < 0.0001$, Fig. 3.1).

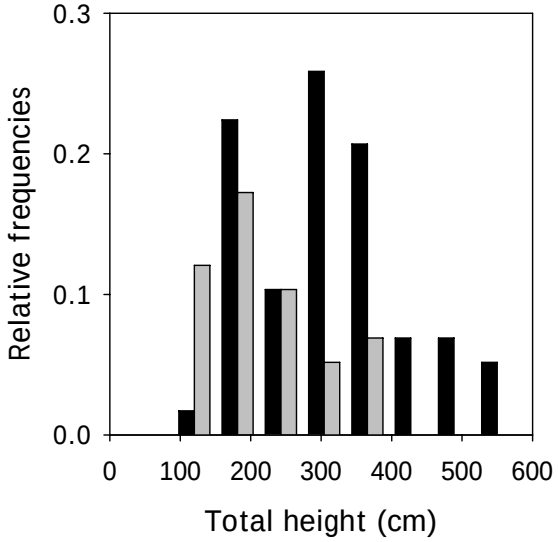

Fig. 3.1: Relative frequencies of total height of *A. mellifera* shrubs without regrowth (black bars, n = 58) and with regrowth after fire (grey bars, n = 30).

Taller live shrubs had taller regrowth (0.9-quantile in Fig. 3.2*a*). This trend can be generalized for all but the 0.5- and the 0.7-quantiles, where the slope of the regression was not significantly greater than 0 (see lower confidence interval in Fig. 3.2*b*). However, the slope of this relationship was only 0.25 (0.9-quantile in Fig. 3.2*a*) and significantly less than 1.00 for all quantiles (see upper confidence interval in Fig. 3.2*b*) so that taller trees had less relative regrowth per unit height than smaller trees. Unmeasured factors had a strong impact on the total height – regrowth height relationship because the upper quantiles did not have the same slope (Fig. 3.2*a*). The effect of the unmeasured factors was interactive rather than additive because the slopes of the quantiles differed greatly (Fig. 3.2*a*).

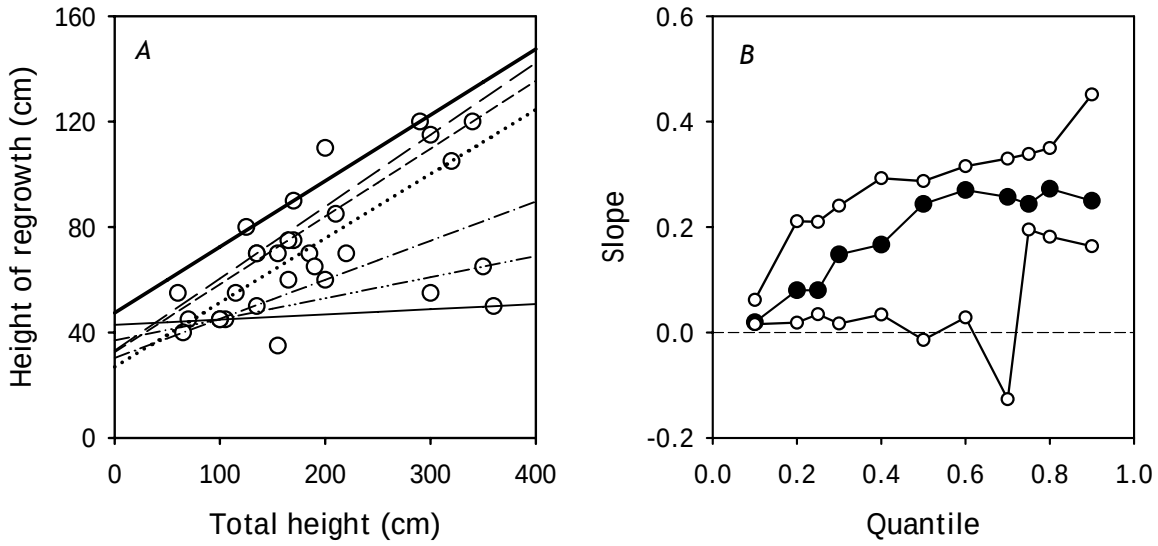

Fig. 3.2: Relationship between the height of regrowth and the total height of *A. mellifera* shrubs (*n* = 30). (*A)* Quantile regression estimates. Quantiles from top to bottom: solid bold line: 0.9-quantile, long-dashed: 0.8-quantile, short-dashed: 0.7-quantile, dotted: 0.5-quantile, dot-dashed: 0.3-quantile, dot-dot-dashed: 0.2-quantile, solid: 0.1-quantile. (*B)* Slope of the quantile regression lines in *a* (solid circles) with upper and lower 90% confidence intervals (open circles).

The relationship between the length of the longest root and the height of a shrub was significantly greater than 0 only for quantiles smaller than or equal to 0.5 (Fig. 3.3). The lower confidence interval of the quantile slopes was significantly larger than 1 only for the 0.1-, 0.3-, and 0.4-quantile (Fig. 3.3*b*). The minimum root length was determined by the height of a shrub but the upper limit is constrained by unmeasured factors.

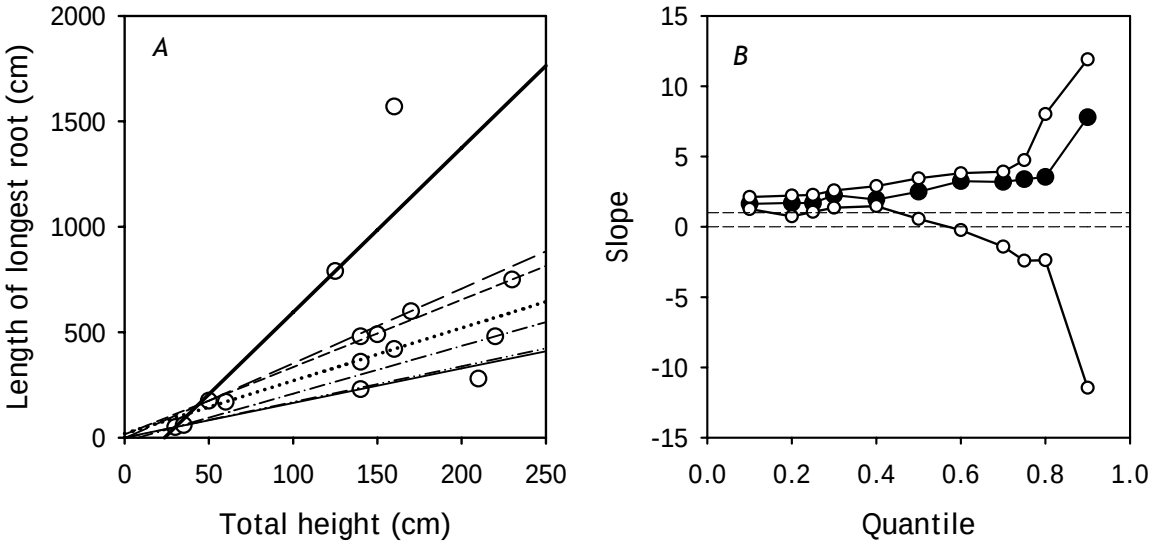

Fig. 3.3: Relationship between the length of the longest root and the total height of *A. mellifera* shrubs (*n*=16). The length of the longest root refers to the maximum length of a surface root between the tap root and the point of turning vertically downwards within a randomly chosen horizontal 60°-angle centered at the tap root. (*A)* Quantile regression estimates. Quantiles from top to bottom: solid bold line: 0.9-quantile, long-dashed: 0.8-quantile, short-dashed: 0.7-quantile, dotted: 0.5-quantile, dot-dashed: 0.3-quantile, dot-dot-dashed: 0.2-quantile, solid: 0.1-quantile. (*B)* Slope of the quantile regression lines in *a* (solid circles) with upper and lower 90% confidence intervals (open circles). The slopes of 0 and 1 (dashed lines) are given as reference lines.

Discussion

Fire did not have a strong impact on *A. mellifera* performance in the study area because mortality after fire is low (9%). Such low mortalities and high resprouting abilities of savanna woody species are in accordance with earlier findings (Keeley *et al.* 1999; Owens *et al.* 2002). The shrubs that were killed completely were significantly taller than their resprouting conspecifics. This is surprising because most studies on size-dependent mortality of savanna woody species reported decreasing post-fire mortalities with increasing size (Hodgkinson 1998; Hoffmann & Solbrig 2003). Adams (1967) has shown that height and shape are reliable indicators of age in *A. mellifera*; consequently, we can conclude that younger *A. mellifera* shrubs have a higher probability of resprouting after fire, which contradicts the general trend in woody species (Turner *et al.* 1999; Seligman & Henkin 2000) but has also been shown for *Adenostoma* shrubs in the chaparral (Odion & Davis 2000).

We can safely assume that taller shrubs have access to disproportionately more below-ground resources than small shrubs due to the positive relationship

between minimum root length and shrub height (Fig. 3.3) and because there is evidence for a positive correlation between stem diameter and below-ground biomass in *Acacia* species (Coughenour *et al.* 1990). In spite of this, smaller *A. mellifera* shrubs have taller relative regrowth per unit height than taller shrubs after fire.

Light, water, and nutrient availability cannot differ greatly between trees of different sizes because all trees grow in the same area. Only small-scale heterogeneities that are correlated with tree size could explain the paradox of less regrowth in taller shrubs in spite of their having more below-ground resources than small shrubs. In general, the importance of environmental factors for shrub regrowth after fire can be doubted: In *Eucalyptus*, the growth rate of resprouting shrubs is primarily determined by physiological and morphological factors associated with plant size and only assisted by greater water and nutrient availability after fire (Hodgkinson 1992).

Another more simple explanation for less regrowth in tall shrubs in spite of more below-ground resources could be that the rate at which new cells can be produced in the apical meristems is physically limited (Lyndon 1976). The proportion of rapidly cycling meristematic cells is strongly correlated with growth (Francis 1998). Thereby, the longitudinal growth rate of a shrub is constrained to a maximum value. This maximum growth rate may have been reached by the regrowth of the taller shrubs in the study area so that the regrowth does not attain the height expected from the total size of the shrubs. Once the maximum longitudinal growth rate is reached, taller shrubs may keep their greater below-ground resources as a reserve or invest them in a greater number of resprouts. In fact, Morrison and Renwick (2000) and Stocker (1999) found that the number of resprouts increased with the size of the stem of several woody species, including *Acacia* shrubs.

Finally, senescence may impair the regrowth of older shrubs. Older shrubs of the Californian chaparral allocate less photosynthate to storage compounds in spring than younger shrubs, indicating a physiological senescence effect (Sparks *et al.* 1993). Senescence effects emerged especially in stands where fire was absent over long periods (Sparks *et al.* 1993), suggesting fire and senescence as rejuvenation agents for plant communities: In other words, an old plant either dies from old age or from fire, thereby making space available for younger plants. If a plants is young enough to survive the fire, it is increasingly affected by physiological disfunctions that accumulate with age and weaken its resprouting

ability. This may explain the relatively lower regrowth in taller (and presumably older) shrubs in the present study.

Our results from the quantile regression also show that unmeasured factors play an important interactive role in the total height - regrowth height relationship. Below-ground biomass, stem diameter, number of resprouts, patchily-distributed resources, and water availability may be among these factors, and should be explored in further research.

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4
Determining patch size

Meyer K. M., Wiegand K., Ward D., Moustakas A. (submitted) *African Journal of Ecology*.

Abstract

Patch-dynamics is a new scale-explicit mechanism explaining tree-grass coexistence in savannas including the ecological and economic problem of shrub encroachment as a natural phase in successional cycles at the patch-scale. We propose a new method for estimating patch sizes based on the canopy diameter and the spatial location of individuals and apply it to an example data set from a semi-arid savanna in South Africa. It is more objective than a morphometric approach of patch size estimation from aerial or satellite pictures or in the field because of a spatial statistical approach, *i.e.*, a canopy filling algorithm combined with a Neyman-Scott cluster process. At the study site, the estimate of the maximum patch diameter was 740 cm which can be multiplied by 4 to also capture the root system extent. If spatial data on root system extents are available, the proposed method can equally well be applied to the estimation of belowground patch sizes.

Keywords

patch-dynamics, shrub encroachment, patch diameter, shrub thicket, savanna, Neyman-Scott cluster process.

Introduction

Shrub encroachment, *i.e.* the increase in density of woody species, is threatening tree-grass coexistence in savannas worldwide (see *e.g.*, Smit 2004; Wiegand *et al.* 2005; Wiegand *et al.* 2006). In addition to ecological problems, shrub encroachment creates economic problems, because it reduces the amount of areas suitable for grazing of livestock. In recognition of the importance of spatial and temporal scales for savannas, Wiegand and colleagues (2005; 2006) proposed patch-dynamics as the driving mechanism of tree-grass coexistence in savannas including a naturally shrub encroached phase. In patch-dynamic landscapes, patches are asynchronously cycling between woody and grassy dominance. Evidence for patch-dynamic savannas is accumulating (*e.g.*, Gillson 2004; Wiegand *et al.* 2006), but simple methods for the determination of the spatial scale of patches are still lacking. In the present study, we propose a method for estimating patch sizes based on the canopy diameter and the spatial location of individuals and apply it to an example data set from a semi-arid savanna in South Africa.

Methods

Method description

To determine the size of patches with the proposed method, canopy diameter and *xy*-coordinates of all shrubs in an area which is in the shrub-dominated phase of the cyclical succession are needed. These can be obtained by direct measurement in the field or from aerial photographs and satellite images.

The proposed method is based on a univariate Neyman-Scott cluster process (Diggle 1983). A Neyman-Scott cluster process is constituted by randomly distributed "parent" points and "offspring" points with a bivariate normal distribution relative to the location of the parent. For the Neyman-Scott process, Ripley's *K*-function and the pair-correlation function g(*h*) (Stoyan & Stoyan 1994) are

$$K(h,\sigma,\rho) = \pi h^2 + \frac{1-e^{(-h^2/4\sigma^2)}}{\rho}$$

and

$$g(h,\sigma,\rho) = 1 + \frac{e^{(-h^2/4\sigma^2)}}{4\pi\sigma^2\rho},$$

where h is the scale investigated, ρ is the intensity of the parent process (*i.e.*, number of points per area), and σ^2 denotes the variance of the distance between each offspring and the parent (Diggle 1983).

Cluster analysis of the stem positions produces biased estimates of patch sizes because shrub cover is also determined by the degree of overlap in canopies. Therefore, we developed an algorithm to fill the canopies (approximated by circles with canopy diameter) with points so that the spatial pattern of the canopies could be analysed. With the canopy filling algorithm, the number of points to be distributed within the borders of each canopy circle was calculated as the area of the canopy circle divided by a square area with side length l. l determines the density of points to be distributed. We suggest using the fifth smallest canopy diameter occurring in the data set for l. The calculated number of points is then randomly distributed within the borders of the canopy circle. Shrub canopies with diameters of less than l are represented by one point only with the original coordinates of the shrub. The overall canopy point pattern is then fitted to a Neyman-Scott process to generate the null model for the confidence interval simulations. The cluster diameter is approximated as 4σ. A confidence level of $p = 0.05$ is obtained when upper and lower confidence envelopes are generated from the 5th greatest and 5th smallest values out of 199 simulations. The *Programmita* software (Wiegand & Moloney 2004) can be used for the fitting and application of the Neyman-Scott model.

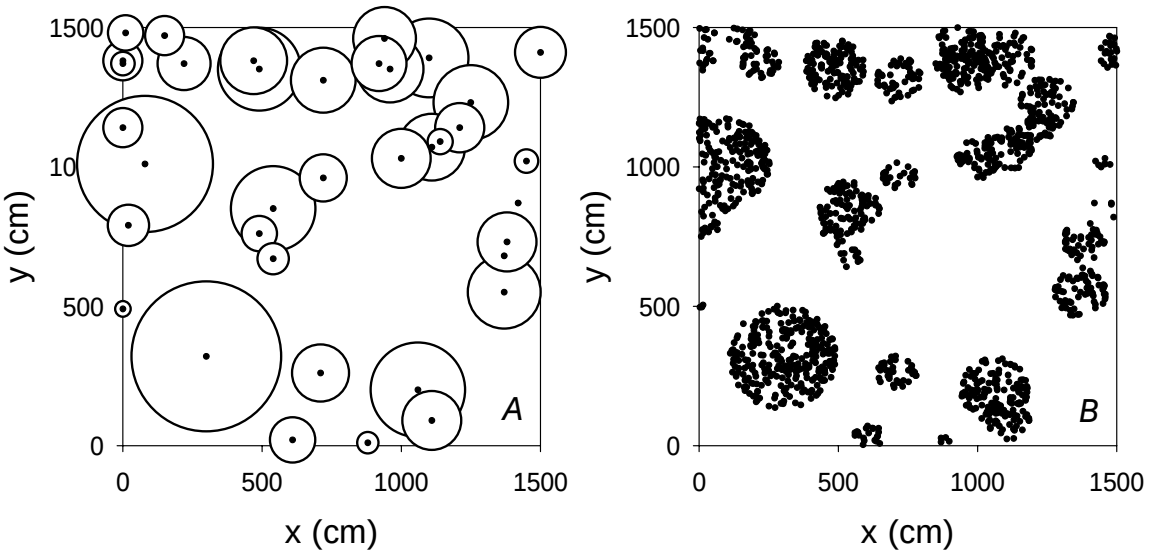

Fig. 4.1: Example of a bird's eye view of one of the 15 m × 15 m example plots. (*A*) *xy*-coordinates of the locations of all shrubs in the plot (solid point in the centre of every circle). The canopy area is approximated by a circle with canopy diameter. (*B*) *xy*-coordinates of the points that were randomly distributed within the borders of the original canopies (see *A*) to allow for the cluster scale calculation.

Application example

The canopy-filling algorithm was applied to spatial data from the Pniel study site in semi-arid savanna in the Kalahari thornveld (S 28° 35', E 24° 29'), 30 km north of Kimberley, South Africa. Within 20 fenced 15 m × 15 m plots, we determined the *xy*-coordinates and the maximum canopy diameter of all shrub individuals (N = 1077, minimum n = 10 shrubs/plot, maximum n = 167 shrubs/plot). Visual inspection of the pattern of the canopies from a bird's eye view revealed clustered shrub patches (Fig. 4.1) fulfilling the prerequisite for the application of the proposed method. We analysed all plots separately with a significance level of p = 0.05.

Results and Discussion

The proposed method is a method for the estimation of patch sizes requiring only information on spatial location and canopy diameters. It is more objective than a morphometric approach of patch size estimation from aerial or satellite pictures or in the field because of the spatial statistical approach. Adding to conventional cluster size estimates (*e.g.*, Plotkin *et al.* 2002), our patch size estimates also include information on canopy cover by including the canopy-filling algorithm.

In the example application, the mean diameter of a cluster approximated 178 cm ±226 cm (S.D.), whereas the maximum cluster diameter was 738 cm, which seem to be rather small patch sizes. Yet, in semi-arid savannas, most interactions occur belowground with root system extents greatly exceeding canopy diameters (root extent > 4 * canopy diameter in *Acacia mellifera*, D. Ward, unpublished result; see also Meyer *et al.* 2005). Thus, real patch sizes may be underestimated in our application. However, if spatial data on root system extents are available, the proposed method can equally well be applied to the estimation of belowground patch sizes. Furthermore, the range of possible applications of the proposed method is not restricted to savannas, but can be applied to any patch size estimation problem in vegetation science.

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5

SATCHMO

A spatial simulation model of growth, competition, and mortality in cycling savanna patches

Meyer K. M., Wiegand K., Ward D., Moustakas A. (in prep.) *Ecological Modelling*.

Abstract

Many mechanisms have been suggested to explain the coexistence of woody species and grasses in savannas, yet, evidence from field studies and simulation models has been mixed. Shrub encroachment is an ecological and economic problem in savannas worldwide which generally is attributed to overgrazing. Patch-dynamics is a new mechanism explaining tree-grass coexistence and the natural occurrence of shrub encroachment in savannas. A patch-dynamic savanna consists of patches in which cyclical succession between grassy and woody dominance proceeds spatially asynchronously. The spatially explicit, individual-based patch-scale simulation model SATCHMO was developed to investigate cyclical succession in the paradigm of patch-dynamics for arid and semi-arid savannas. SATCHMO is designed to capture within-patch shrub population dynamics based on a grid of 51 m side-length and a resolution of 10 cm. The model shrub characteristics were derived from *Acacia mellifera*, the main encroaching species in African savannas. The aim of SATCHMO is to give a detailed small-scale understanding of above- and belowground growth, competition, and mortality of savanna woody plants and the influence of precipitation and fire on patch transition frequencies, shrub growth rates, and shrub size-frequencies. With SATCHMO, we want to identify the conditions leading to cyclical successions in general and shrub encroachment in particular. Soil moisture is the central parameter in SATCHMO influencing growth, reproduction, and mortality of shrubs and grass tufts, and that mediates competition. To acknowledge the importance of belowground interactions in savannas, shrub root growth and competition are modelled spatially explicitly. The model output was successfully validated with morphometrical and spatial data from the field site in the South African Kalahari thornveld and with recent literature data on savanna woody species cover. Global sensitivity analysis with Latin hypercube sampling shows that soil moisture is the most important driver of shrub cover dynamics in semi-arid savannas.

Introduction

Savannas are ecosystems co-dominated by woody species and grasses in varying relative proportions. The widely discussed 'savanna question' is concerned with the factors that promote tree-grass coexistence and prevent savannas from being driven to open grassland or forests with a closed canopy. Many empirical studies and savanna models have proposed solutions to the savanna question (Walter 1971; Walker *et al*. 1981; Walker & Noy-Meir 1982; Eagleson & Segarra 1985; Menaut *et al*. 1990; Hochberg *et al*. 1994; Jeltsch *et al*. 1996; Jeltsch *et al*. 1998; Higgins *et al*. 2000; Jeltsch *et al*. 2000; Fernandez-Illescas *et al*. 2001; van Wijk & Bouten 2001; van Langevelde *et al*. 2003). In the majority of studies, there is agreement on the four key factors determining savanna dynamics: water, nutrients, herbivory, and fire (Frost *et al*. 1986; Sankaran *et al*. 2004), but their relative importance has long been unclear. Recently, the analysis of data from 854 African field sites showed the paramount impact of mean annual precipitation (MAP) on woody cover as a switch effect at 650 mm MAP (Sankaran *et al*. 2005). Below this threshold, in arid and semi-arid savannas, herbivory, fire, and soil properties can only reduce woody cover below its maximum which depends linearly on MAP. Above this threshold, savannas are unstable and disturbances such as fire or herbivory are necessary to prevent canopy closure (Sankaran *et al*. 2005). The dominant role of water among the key determinants of savanna structure also highlights the greater importance of belowground interactions in arid and semi-arid savannas compared to aboveground interactions. Unfortunately, field methods for belowground investigations come at a much greater cost than aboveground methods so that simulation models provide an efficient alternative for capturing a reasonable amount of detail with similar effort for above- or belowground systems.

With respect to the mechanisms underlying tree-grass coexistence, both empirical evidence and model results are mixed and emphasize different aspects of savanna dynamics for the explanation of tree-grass coexistence. In their comprehensive review of savanna models, Sankaran *et al*. (2004) consider explanations focusing on the limiting role of demographic bottlenecks in woody species populations (Higgins *et al*. 2000; Jeltsch *et al*. 2000) to be superior to the traditional competition-based explanations (Walter 1971; Walker *et al*. 1981; Walker & Noy-Meir 1982; Eagleson & Segarra 1985) because empirical evidence for rooting niche separation and other competitive mechanisms is equivocal (Scholes & Archer 1997; Sankaran *et al*. 2004; Wiegand *et al*. 2005) and resource competition alone does not produce coexistence in spatially explicit models (Jeltsch *et al*.

2000). Still, a unifying mechanism explaining tree-grass coexistence in savannas is lacking.

Furthermore, the 'savanna question' is not only an ecological issue but also has a socio-economic dimension. Shrub encroachment, *i.e.*, the increase in density of woody plants often unpalatable to livestock, is observed in savannas all over the world reducing the amount and quality of grazing lands dramatically. So far, it was generally believed that overgrazing in combination with rooting-niche separation is primarily responsible for shrub encroachment. However, recent research has not only questioned the universality of the rooting-niche-separation in particular and competition-based models in general but also the paramount importance of overgrazing for fostering shrub encroachment (Wiegand *et al*. 2005; Wiegand *et al*. 2006).

Wiegand *et al*. (2006) propose the patch-dynamics paradigm as a mechanism explaining tree-grass coexistence in arid savannas. The patch-dynamics concept is based on a cyclical succession that proceeds asynchronously in spatially distinct patches that constitute the savanna landscape. Patches cycle between woody and grassy dominance so that shrub encroachment is a natural phase in the cyclical succession. Patch-dynamics and overgrazing are not mutually exclusive explanations for shrub encroachment, but may enhance each other. If overgrazing occurs during the naturally encroached phase of the successional cycle, its effect on shrub cover increase will be greater than if it occurred during a non-encroached phase of the cycle. Moreover, the patch-dynamics paradigm does not exclude other theories about tree-grass coexistence, but can integrate many of the savanna theories put forward thus far because cyclical succession can be driven by a range of processes. For instance, the spatial and temporal overlap of localised rain events in arid savannas may induce mass germination of a shrub cohort and promote the transition of a grass-dominated patch to woody dominance. Empirical support for patch-dynamics is offered from paleoecological long-term studies in east African savannas that revealed cyclical changes in the relative abundance of trees and grasses at the local scale but stable proportions at the landscape scale (Gillson 2004). The advantage - but also the challenge - of the patch-dynamics concept is its explicit consideration of spatial and temporal scales. While field studies are rarely able to cover several spatial and temporal scales (but see Gillson 2004), simulation models do not suffer from such restrictions. In simulation models, processes can be implemented at one scale generating patterns at the next greater scale (Jeltsch *et al*. 1996; Wiegand *et al*. 2003). For this procedure to be

successful, the processes prevailing at small scales have to be understood in detail before they can be generalized to larger scales. The great amount of detail necessary for a good understanding of small-scale processes with simulation models is supported by the accessibility of small-scale field data for model parameterization relative to data at larger scales.

In order to investigate cyclical succession at the patch-scale, we developed the small-scale spatially explicit, individual-based Savanna pATCH MOdel SATCHMO for arid and semi-arid savannas (MAP < 650 mm). The focus of our model lies on savannas that receive less than 650 mm MAP because the continental-scale analysis of Sankaran *et al.* (2005) shows that water is the most limiting factor for woody cover and permits tree-grass-coexistence in these savannas. The purpose of SATCHMO is to model within-patch population dynamics that give a detailed small-scale understanding of above- and belowground growth, competition, and mortality of savanna woody plants and the conditions leading to cyclical successions in general and shrub encroachment in particular.

Methods

I. Study area

SATCHMO is based on field data that were collected in semi-arid savanna in the Kalahari thornveld at Pniel Estates (S 28° 35', E 24° 29'), 30 km north of Kimberley, South Africa, between 2003 and 2005 (see also Meyer *et al.* 2005; Chapter 2). Mean annual precipitation is 377 mm and mostly occurs as thunderstorms throughout the summer months (September to March). Blackthorn (*Acacia mellifera*) is the dominant plant species in the study area; camphor trees (*Tarchonanthus camphoratus*) and umbrella thorns (*A. tortilis*) are other important woody species.

II. Model description

The model description follows the PSPC+3 protocol for describing individual-based simulation models (Grimm *et al.* in press).

State variables and scales

The basic objects in SATCHMO are a shrub, a grass tuft, and the root of a shrub. Until the age of one year, shrubs and grasses are referred to as seedlings, thereafter as established shrubs and grass tufts.

Shrubs were modelled following the characteristics of the dominant species in the area, because one aim of SATCHMO is to identify conditions leading to shrub encroachment. Individual shrubs are characterized by the state variables location (*xy*-coordinate), canopy diameter, height, age, root system radius, and width of uptake zone. Each root is surrounded by an uptake zone in which water uptake occurs. If the uptake zones of two roots meet, an interaction scenario is activated. In scenarios with competition, the width of the uptake zone is a measure of the territoriality of the shrub. Aboveground, shrubs older than one year are represented by a circle with canopy diameter as diameter.

To acknowledge the predominant importance of soil moisture mediating plant interactions in semi-arid savannas, we modelled shrub roots spatially explicitly in two dimensions. We simplify the shrub root system by representing it with eight horizontal roots which initially radiate from the shrub base in the cardinal and intermediate directions at angles of 45° (Fig. 5.1). Roots are characterized by the state variables number and location of the shrub they belong to, root number (1 to 8), *xy*-coordinates of the most distant and second most distant cell of the root, whether they have stopped to grow, and whether they grow in cardinal or intermediate direction. Roots are surrounded by an uptake zone whose width approximates the length of side roots responsible for water uptake.

Grass tufts serve as interspecific competitors for the shrubs. The grass state variables are individual number, location (*xy*-coordinate), canopy diameter, age, and width of uptake zone. Aboveground, grass tufts are represented by a circle with canopy diameter. Grass roots were not modelled spatially explicitly because grass was not in the focus of the model and because information on grass roots is scarce. Instead, water uptake occurs in a circular uptake zone around the canopy.

On a higher hierarchical level, all shrubs and all grasses in the simulated area constitute one population each. Populations are characterized by their number of individuals, the percentage ground covered by all canopies, and their canopy diameter-frequency distributions. Model outputs were analysed at the level of individuals and populations.

SATCHMO is based on a two-dimensional grid with 512 x 512 cells. The spatial extent of the grid corresponds to 51.2 m in reality. This side length corresponds to the sum of the maximum diameter of a shrub thicket (=patch) in the field of about 8 m, the maximum diameter of a shrub root system excavated in the study area of about 32 m (Meyer *et al*. 2005), and a buffer of about 10 m for patch edge effects.

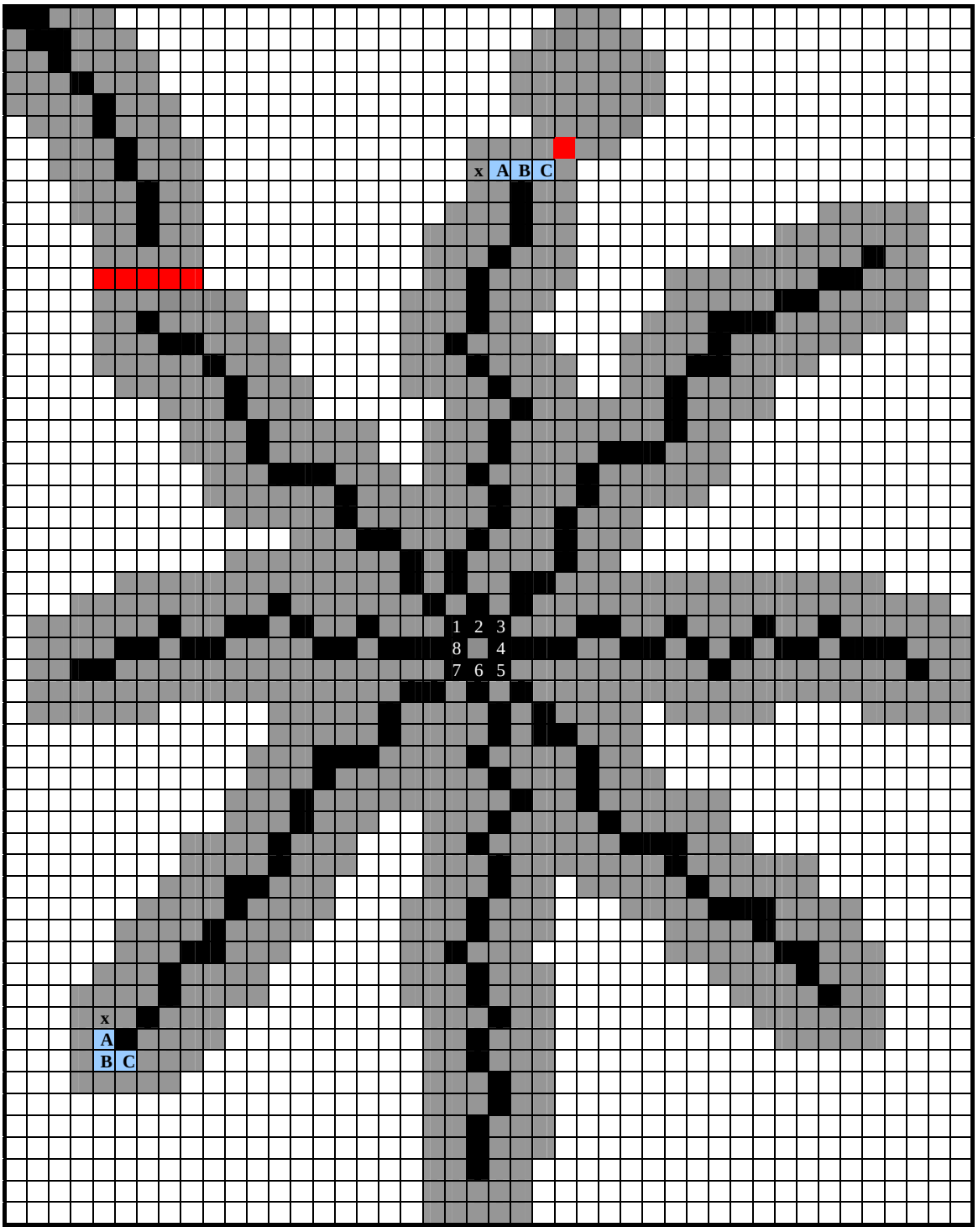

Fig. 5.1: Schematic representation of belowground characteristics of a model shrub competing with a grass tuft (top right) and a root from another shrub (top left). The eight roots (black cells) of the model shrub are surrounded by their uptake zone (grey cells) with a width of two cells where water uptake occurs. If the uptake zone overlaps with uptake zones of other shrubs or grasses (red cells) competition takes place. Shrubs compete only indirectly with grasses by sharing the soil moisture in the overlapping cells. If two uptake zones of shrub roots meet, the result is determined by the competition scenario. Numbers 1 to 8 refer to the starting point of the eight roots. The letters A, B, and C mark the possible cells to grow into (light blue cells) during the next growth step in descending probability order for a root with cardinal original growing direction (number 2) and one with intermediate original growing direction (number 7). The X marks the original growing direction.

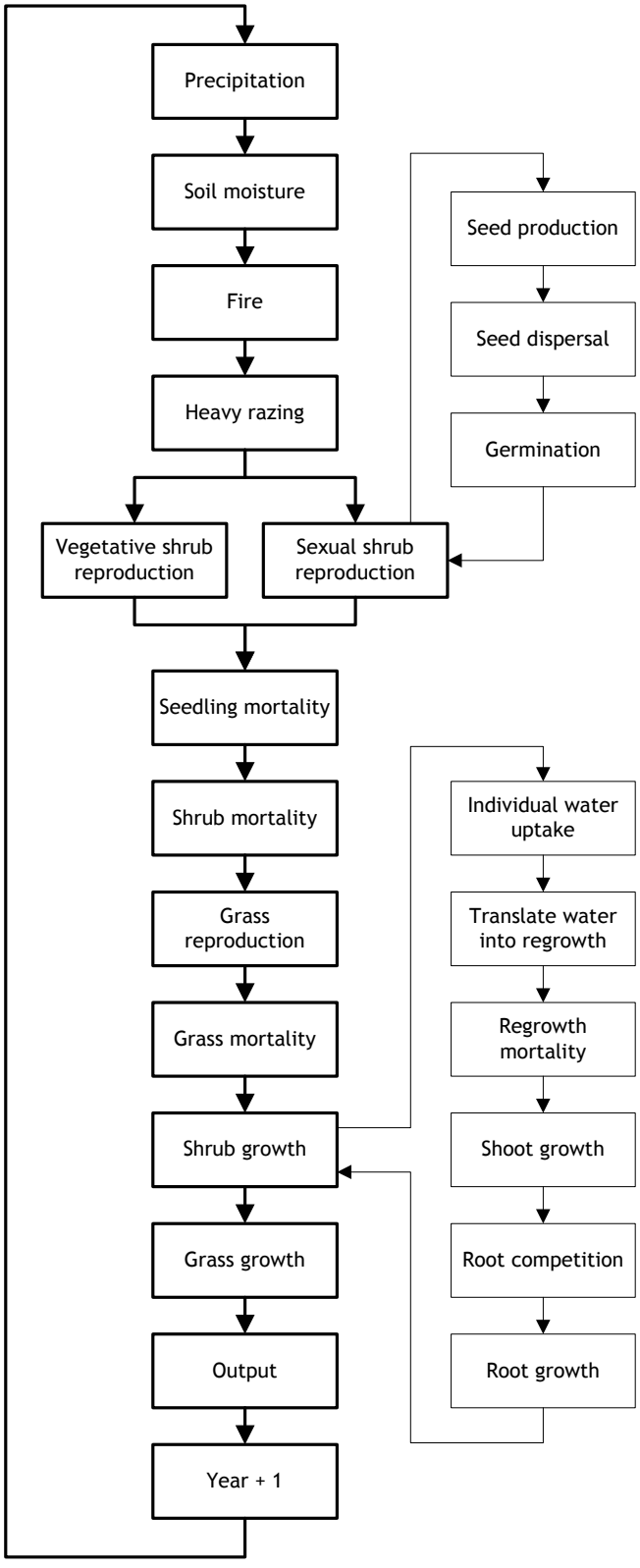

Fig. 5.2: Scheduling of the main processes in SATCHMO.

The side length of one cell corresponds to 10 cm which is the greatest common accuracy of all morphometric measurements in the field. We do not model soil depth explicitly because the roots of the plants modelled predominantly occur in the topmost soil layer where also the greatest part of the soil moisture and virtually all nutrients are restricted to (Evans & Ehleringer 1993). The temporal resolution is daily for precipitation and annual for shrub and grass dynamics. The temporal extent of the simulations is 500 years to capture long-term savanna dynamics.

Process overview and scheduling

In SATCHMO, environmental processes (precipitation, soil moisture, and fire) are followed by the individual processes of shrub reproduction and mortality, grass reproduction and mortality, and shrub and grass growth (Fig. 5.2; for a detailed description of the model processes refer to the section *Submodels*). Sexual reproduction includes seed production, seed dispersal, and germination. Shrub growth is the core module of SATCHMO where above- and belowground regrowth are derived from individual water uptake, leading to mortality if regrowth is negative and to shoot and root growth if regrowth is positive. Root growth may be impaired in several mutually exclusive root competition scenarios. Time proceeds in discrete time steps (daily for precipitation, annual for all other processes).

Design concepts

Emergence. – Maximum shrub age is an emergent property of SATCHMO, as well as population size and spatial shrub and grass patterns and all other population-level characteristics.

Sensing. – Individual shrubs sense the soil moisture in the cells covered by their root uptake zones, their own height to produce the corresponding number of seeds, their location for aggregated seed dispersal, and their own canopy diameter as a proxy for maintenance costs in the calculation of regrowth from water uptake. Roots sense their original direction (cardinal or intermediate) and the contact of their uptake zone with the uptake zone of another root.

Interaction. – Shrubs whose uptake zones overlap with other shrubs or grasses interact by sharing the soil moisture in the overlapping cells. If two uptake zones meet, the kind of interaction is determined by the specified competition scenario (see submodel *Root growth*). Aboveground contact of shrub or grass canopies does not lead to interactions.

Table 5.1: SATCHMO model parameters.[†]

Parameter	Accur	Default	Source	Range	Distr	Source	Std RC N	Std RC Cover
Soil moisture parameters								
Long-term mean annual rainfall (mm)	1	377	Kimberley	203 - 553	n	SD, Pniel	ns	2.35
Long-term S.D. of annual rainfall (mm)	1	174	Kimberley	-	-	-	-	-
Interception $D(t)$ of grasses (mm)	3	1	Ref1	0.9 – 1.1	u	10%, EG	ns	ns
Interception $D(t)$ of shrubs (mm)	3	1.5	Ref1	0.85 – 1.15	u	10%, EG	6.79	3.65
Evapotranspiration E_{max} (mm)	2	8	Kimberley[1]	7.1 - 8.9	n	SD, Kimberley	2.89	ns
Critical soil saturation s_c for grasses*	3	0.35	Ref2	0.15 – 0.5	e	Ref3	ns	ns
Critical soil saturation s_c for shrubs*	3	0.33	Ref2	0.15 – 0.5	e	Ref3	4.35	ns
Critical soil saturation s_c for bare ground*	3	0.33	Ref2	0.15 – 0.5	e	Ref3	ns	ns
Soil field capacity s_{fc}*	2	0.442	Pniel	0.398 – 0.482	u	10%, EG	5.72	2.34
Soil porosity n*	3	0.373	Ref4	0.373 - 0.48	e	Ref4	ns	ns
Maximum rooting depth Z (mm)	2	700	Pniel	150 - 1050	u	Min-Max, Pniel	5.08	4.71
Relative water uptake of plants in grid cell	4	0.9	EG	0.81 – 0.99	u	10%, EG	3.73	2.79
Fire parameters								
Fire frequency (year^{-1})	2	0.006	Pniel	0.0006 – 0.06	e	*/10, EG	ns	ns
Maximum fire frequency (year^{-1})	2	1	Pniel	-	-	-	-	-
Shrub reproduction parameters								
Cumulative seed moisture threshold[2]	3	2.35	Kimberley	0.86 – 2.35	u	Min-Max, Kimberley	6.72	5.32

Table 1 cont.

Cumulative shrub germination moisture threshold[3]	3	0.128	Kimberley	0.07 – 0.228	e	Min, Kimberley Max, EG	ns	ns
Shrub germination rain event (days)	4	3	Kimberley	-	-	-	-	-
Shrub germination probability	2	0.19	Pniel	0.09 – 0.19	u	Min-Max, Pniel	ns	ns
Vegetative reproduction probability	4	0.0005	EG	0.00005 – 0.05	e	*/100, EG	ns	ns
Number of vegetative seedlings (shrub^{-1})	4	15	EG	-	-	-	-	-
Shrub mortality parameters								
Seedling mortality coefficient *a* (10^6)	3	75.953	Pniel	75.953 – 7595.3	u	Min, Pniel Max, *100	2.39	ns
Fire mortality of seedlings	4	0.65	EG	0.5 – 0.95	n	EG	ns	ns
Natural browsing mortality of seedlings	4	0.95	EG	0.5 – 0.999	e	EG	12.34	3.84
Basic mortality of established shrubs (10^{-3})	2	6.5	Ref5, Ref9	5.85 – 7.15	e	10%, EG	ns	ns
Fire mortality of established shrubs	1	0.09	Ref6	0.081 – 0.099	e	10%, EG	ns	ns
Drought mortality of established shrubs	4	0.05	EG	0.04 – 0.06	u	20%, EG	ns	ns
Shrub growth parameters								
Regrowth probability	2	0.55	Pniel	0.46 – 0.62	u	Min-Max, Pniel	ns	ns
Line probability[4]	4	0.5	EG	0 - 1	n	EG	ns	ns
Width of shrub uptake zone (cells)	2	2	EG[5]	-	-	-	-	-
Competition scenario	4	asymm	EG	-	-	-	-	-

Table 1 cont.

Grass demography parameters								
Grass germination moisture[3]	3	0.128	Kimberley	0.07 – 0.228	e	Min, Kimberley Max, EG	3.09	3.20
Grass germination rain event (days)	4	3	Kimberley	-	-	-	-	-
Number of grass seedlings (m^{-2})	3	2.35	Ref7[6]	-	-	-	-	-
Grass seedling survival	3	0.72	Ref7[6]	0.65 – 0.79	n	10%, EG	ns	ns
Grass mortality	3	0.47	Ref8 [6]	0.42 – 0.52	n	10%, EG	5.61	3.84
Grass regrowth length (cm)	3	5	Ref8	-	-	-	-	-
Width of grass uptake zone (cells)	3	2	EG[5]	-	-	-	-	-
Technical parameters								
Time steps (years)	-	800	Fig. 5.3	-	-	-	-	-
Number of runs	-	10	Results	-	-	-	-	-

[†] Default – standard values of the parameters of SATCHMO, Accur - estimated accuracy of standard values, Source – sources of standard values, Range – range from which values were sampled for sensitivity analysis, Distr - distributions from which values were sampled for sensitivity analysis, Source – sources of ranges and distributions, Std RC - standardized regression coefficients representing the sensitivity of shrub cover (Cover) and shrub population size (N) to changes in the parameter values, * refers to sandy soil which is the main soil type of the study site at Pniel Estates, [1] long-term average evaporation, [2] minimum cumulative soil moisture between September and November needed for seed production, [3] minimum cumulative soil moisture per germination rain event between December and March needed for triggering germination, [4] probability of a root to maintain its growing direction, [5] corresponding to 20 cm length of (side) roots, [6] calculated with a mean annual precipitation of 377 mm (Kimberley weather data), asymm – asymmetric competition scenario, accuracy scale: 1 – very well known, 2 – well known, 3 – approximately known, 4 – not well known, Ref1 - (Scholes & Walker 1993), Ref2 - (Laio *et al*. 2001), Ref3 - (Rodriguez-Iturbe *et al*. 1999), Ref4 - (Fernandez-Illescas *et al*. 2001), Ref5 – Chapter 2, Ref6 - (Meyer *et al*. 2005), Ref7 - (O'Connor 1994), Ref8 - (O'Connor & Everson 1998), Ref9 - (Augustine & Mcnaughton 2004), Pniel – estimated from Pniel field data, Kimberley – estimated from Kimberley weather data, n – normal distributin, u – uniform distribution, e – exponential distribution, EG – expert guesses, SD – range refers to standard deviation, 10% or 20% - range refers to +/-10% or 20%, */10 – range refers to *10 and /10, Min-Max – range refers to minimum and maximum, ns – not significant.

Stochasticity. – All demographic parameters include stochasticity by handling them as probabilities to incorporate individual variability. Root growth follows a weighted random walk so that deviations of one cell to the right and to the left of the original growing direction of the root are possible (but less probable) than the original direction (see *line probability* in Table 5.1).

Observation. – Individual shrub characteristics such as canopy diameter, height, age, location, and root system radius are determined every five years. Individual grass characteristics are collected every 100 years. Population-level outputs, i.e. population size and shrub and grass cover, are generated at the end of every year.

Initialization

Initially, one reproductively mature shrub with a height of 130 cm and a canopy diameter of 184.75 cm is located in the centre of the grid supplemented by ten randomly-arranged grass tufts whose canopy diameters are drawn from a normal distribution with mean and standard deviation from field data (20.88 +/- 15.79 cm). The length of the shrub roots is calculated as a random number between the 0.9- and 0.5-quantile of the quantile regression of root length and shrub canopy diameter (Meyer *et al*. 2005). We included only quantiles for which the slope of the regression was significantly different from 0. Roots are initialized as if they had maintained their original direction without random deviation until the calculated root length was reached. Based on an asymptotic model of shrub cover over time (Fig. 5.3), model evaluation started after 300 years of pre-simulation to exclude an influence of initial conditions.

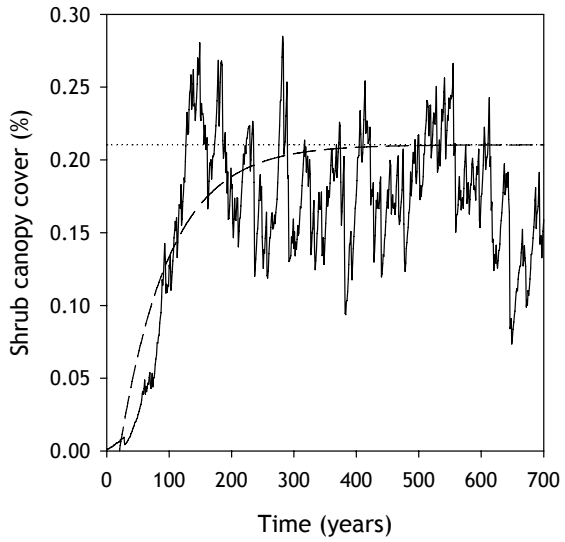

Fig. 5.3: Simulated shrub canopy cover in % over time (solid line) with asymptotic regression model (dashed line). To exclude an effect of initial conditions, model evaluation starts only at year 300 when the regression line is sufficiently close to the asymptote (dottet line).

Input

Input environmental conditions that affect the state variables in SATCHMO are precipitation and fire. In semi-arid savannas, water limits plant growth much more than nutrients, and still noticeably more than fire or grazing (Sankaran *et al.* 2005). Hence, we do not explicitly take nutrient dynamics and grazing into account and model fire with less detail.

A daily precipitation value is calculated for the model grid according to the Zucchini-algorithm for South-African rainfall (Zucchini *et al.* 1992). The parameterization of this algorithm is based on weather data from Kimberley, the closest weather station to the field sites.

In semi-arid savannas, fire is of minor importance compared to moister savannas because there is insufficient grass biomass present to fuel frequent and intense fires (Bond & Van Wilgen 1996; Higgins *et al.* 2000). Hence, in SATCHMO, fire is characterised by its average (0.006 $year^{-1}$) and maximum (1 $year^{-1}$) frequency (Table 5.1). The standard value of fire frequency is derived from a space-for-time substitution: at the study site of 22000 ha in total, during the last three years, only one fire was observed affecting 400 ha (Meyer *et al.* 2005), giving a fire frequency of 0.006 $year^{-1}$ for the whole area. The occurrence of a fire leads to increased mortalities in established shrubs and especially in shrub seedlings. Shrub growth is not impaired by fire because *A. mellifera* can compensate for losses by regrowth from the stem bases (Donaldson 1967). Grass mortality and growth are not modified by the occurrence of a fire because grasses will have compensated for biomass losses until the end of the vegetation period (Noy-Meir 1995; Van de Vijver *et al.* 1999).

Grazing and browsing are not modelled explicitly (*e.g.*, via stocking densities) because the field data underlying SATCHMO were collected in areas with natural grazing intensities so that grazing effects are implicitly included in the parameterization of SATCHMO. On the other hand, overgrazing scenarios are not included because the focus of SATCHMO is on the investigation of natural drivers of shrub encroachment.

Submodels

Soil moisture. – From precipitation, soil moisture is calculated independently for each grid cell, because local soil moisture can differ in the presence of roots or canopies which influence soil moisture availability through interception and the amount of moisture left after water uptake. Soil moisture is

the basic currency of the model mediating competition, growth, and some aspects of mortality and reproduction. Temporal soil moisture dynamics is modelled as

$$\frac{\Delta s(t)}{\Delta t} = \frac{R(t)}{nZ} - \frac{D(t)}{nZ} - \frac{E(s(t),t)}{nZ} - \frac{L(s(t),t)}{nZ} \quad (1)$$

where $s(t)$ is the relative moisture content of a cell, t is the time step (daily), n is soil porosity, Z is the depth of active soil or rooting depth, $R(t)$ is the amount of incoming rain, $D(t)$ is the amount of incoming rain lost through interception by canopy cover, evapotranspiration $E(s(t),t)$ is the amount of water lost through transpiration of plants and evaporation of bare ground, and $L(s(t),t)$ is leakage to deeper soil layers (Table 5.1). Surface runoff is not included because the field data were collected in a reasonably flat area so that it can be assumed that inflow and outflow balance each other. The algorithm for the calculation of soil moisture for a specific cell with residual soil moisture from the previous day $s(t\text{-}1)$ follows roughly Rodriguez-Iturbe *et al.* (1999, see also Appendix A).

Shrub reproduction. - Shrubs can reproduce vegetatively and sexually. Sexual reproduction involves seed production, seed dispersal, germination, and seedling mortality. Seed production and germination can be initiated only after certain cumulative soil moisture thresholds are exceeded (Table 5.1). For seed production, this threshold is defined by the total cumulative soil moisture between September and November. For parameterization of SATCHMO, the seed production threshold was determined conservatively from regional weather data from 2004 when seed production was observed at the study site (contrarily to 2003 when no seed production occurred and cumulative moisture was much smaller). The number of seeds per shrub depends on its size and is determined from the empirical relationship

Number of seeds = 22.98 * height (cm) – 2380 (2)

which also defines the minimum height for seed production (104 cm, r^2=0.72, D.Ward, unpublished data). Every shrub taller than 104 cm can produce seeds.

Seed dispersal includes aggregated short-distance dispersal and random long-distance dispersal. Based on seed-dispersal distances assembled from two shrubs in the study area, 60% of the seeds of a shrub are randomly distributed within its canopy radius, another 35% are randomly distributed within the radius and twice the radius, and the remaining 5% are pooled for all seed-producing shrubs and then randomly distributed in the whole grid to account for long-distance dispersal. This also is close to an exponential decline (Okubo & Levin 1989; Witkowski & Garner 2000). To include intraspecific competition, only one seed per

cell (100 cm^2) is allowed. Assuming that the number of seeds leaving the grid will be balanced by the number of seeds entering the grid, we applied toroidal edge correction.

Germination of shrub seedlings occurs only if the cumulative soil moisture of a certain number of successive days exceeds the germination threshold (Table 5.1). The germination soil moisture threshold and the number of days were determined from the closest rain flush prior to the germination event observed at the study site in January 2005. Whether the moisture threshold is reached may vary from cell to cell. If the threshold is exceeded, seeds germinate according to the germination probability determined in an experiment at the field site in 2005. In this experiment, *A. mellifera* seeds were sown in 14 2 m x 2 m plots at a density of 400 seeds per plot. Half of the plots were cut to simulate heavy grazing, the other half was left uncut as controls. The plots were watered every two to three days to field capacity. Germination rate was 0.19, and we did not find significant differences between cut and uncut plots (t=-0.33, df=1, p=0.37). Germination does not depend on temperature because temperature is not a limiting factor at the field site in summer when germination occurs.

Although genetic analyses indicate that vegetative reproduction may occur in *A. mellifera* (B. Nxele, unpublished results), we did not find any evidence for rhizome resprouting during root excavations of close neighbours (Meyer *et al.* 2005). To account for this in SATCHMO, vegetative and sexual reproduction are mutually exclusive within one year and the probability of vegetative reproduction and the numbers of resprouts are very low (Table 5.1). If vegetative reproduction occurs, the respective number of resprouts is randomly distributed within the root system radius of the individual.

Shrub seedling mortality. – The basic seedling mortality depends on the soil moisture in the cell where the seedling is located following the equation

$$\text{Seedling mortality} = m^{(-\ \text{soil moisture})} \quad (3)$$

where m is the seedling mortality coefficient which was determined from the germination experiment described above. After one year, no seedling had died of the 3041 seeds that germinated in the experiment which was watered to field capacity (0.442). Conservatively assuming that the next seedling would have died, we determined m from the empirical relationship

$$1/3042 = m^{(-\ 0.442)}\ . \quad (4)$$

To account for the strong influence of herbivory on vulnerable seedlings, we included an additional natural browsing mortality (Table 5.1). If a fire occurs, seedlings are affected by an extra fire mortality (Table 5.1).

Shrub mortality. - The basic annual shrub mortality (Table 5.1) is not modelled explicitly but included into the growth submodel so that the mortality emerging from negative regrowth does not exceed the empirically found mortality (see section *Shrub growth*). The size-frequency distributions of dead and alive shrubs did not differ significantly (Wilcoxon's signed rank test, $p = 0.06$, but note the small sample size of dead shrubs $n = 3$), so that basic shrub mortality was not modelled size-dependent. Additional mortality occurs through fire and droughts (Table 5.1). A drought year is defined as a year with less than the long-term mean annual precipitation minus one standard deviation. Drought mortality also includes mortality due to browsing because browsing of *A. mellifera* usually occurs in dry periods. If a shrub dies, the shrub and its roots and uptake zone are removed from the simulation.

Grass reproduction. - Grass population dynamics is modelled with less detail than shrub population dynamics because grass was not in the focus of the model and data on individual grass tufts are scarce. The parameterization of the grass submodels in SATCHMO relies entirely on literature data which was adapted to our field site conditions via the long-term annual mean precipitation. We assume that only perennial grasses are present. We do not differentiate between sexual and vegetative reproduction because grasses with stoloniferous or rhizomatous growth do not necessarily produce fewer seeds than seed-producing grasses (O'Connor 1992). When the reproduction soil moisture threshold is reached, a fixed density of new grass tufts is distributed randomly over the whole grid (Table 5.1). This reproduction soil moisture threshold is equal to the germination moisture threshold of shrubs (see above).

Grass mortality. - Grass seedling mortality applies to all new grass tufts whereas grass tuft mortality is applied to all tufts older than one year (Table 5.1). We do not include an extra fire mortality because tiller losses due to fire are compensated until the end of the growing season (Silva & Raventos 1999).

Shrub growth. – To model the growth of their first two years, new shrub seedlings (age 0 and 1) are deterministically initialized with eight roots starting in the eight cells surrounding the seedling's centre (*xy*-location) and further occupying every second cell in the second row around the seedling's centre. Thereby, the eight roots alternately are assigned an originally cardinal or

intermediate growth direction. It follows that the initial maximum root system radius of all seedlings is twice the diagonal length of a cell, *i.e.,* 28.28 cm for a cell size of 10 cm. Resulting from the empirical relationship between root length and canopy diameter (0.5-quantile in Fig. 3a in Meyer *et al*. 2005), the initial canopy diameter of seedlings deterministically is set to 6.23 cm giving an initial height of 12.43 cm.

For all shrubs older than one year, individual water uptake is calculated by iterating over all cells in the grid and distributing the absolute soil moisture (in mm) in each cell at equal parts to all shrubs and grasses whose uptake zone covers the cell. We assume that plants cannot extract all soil moisture from a cell due to physical reasons, so that only a specified proportion of the soil moisture is distributed (*relative water uptake* in Table 5.1).

Whether the total amount of water taken up by a shrub is translated into regrowth is specified by the regrowth probability (Table 5.1). The regrowth probability was estimated from the average proportion of regrowing shrubs at the field site in two consecutive years (n = 282 shrubs). Whether a shrub produced regrowth in the second year did not depend on whether it had produced regrowth in the first year (Spearman's rank correlation, *rho* = 0.28).

If a shrub does produce regrowth, regrowth length is determined following the rationale that the resources taken up have to be used for maintenance of the plant body, reproduction, and above- and belowground growth. We use moisture as a proxy for resources, canopy diameter as a proxy for maintenance, seed number as a proxy for reproductive effort, and regrowth length as a proxy for growth. Based on approximations from field data, we fitted linear models with square-root transformed moisture for seed-producing shrubs and for shrubs without seed production (see Appendix B for a detailed account of the fitting procedure).

We fitted the following models with square-root transformed moisture and shoot regrowth as an offset to ensure a realistic shoot regrowth range (corresponding to equations (B2) and (B3) in Appendix B):

1. For seed-producing shrubs:

$$\text{Root growth} = 4.22*\text{shoot growth} + 0.0, \quad (5)$$

$$\text{Shoot growth} = (\text{moisture}^{0.5} - 2.49*\text{canopy diameter} + 0.17*\text{seeds} + 358.60 + 0.20*0.0) / (1.0 - 0.20*4.22) \quad (6)$$

2. For shrubs that have not produced seeds:

Root growth = 4.54*shoot growth + 0.0, (7)

Shoot growth = (moisture$^{0.5}$ – 0.01*canopy diameter – 0.44 + 0.18*0.0) / (1.0 - 0.18*4.54). (8)

To account for the competitive effects that were not included into the moisture calculations and to ensure that the emergent mortality of established shrubs matches the empirically determined mortality, only those shrubs die that have a shoot growth of less than 0 minus a certain buffer. The buffer is determined separately for seed-producers and non-seed-producers by recalculating the shoot growth of the data set with the equations (6) and (8) and arranging shrubs with negative regrowth values in descending order. The value of the buffer is equal to the *x*th lowest absolute regrowth value of the ordered shrubs where *x* is the basic mortality of established shrubs multiplied with the number of shrubs with negative regrowth. Through this procedure, the line of zero regrowth is lowered by the value of the buffer, so that the actual regrowth length is obtained from the sum of the regrowth calculated with equations (6) or (8) and the buffer.

For shoot growth, twice the actual regrowth length is added to the canopy diameter of the shrub (because empirically determined regrowth refers to canopy radius) and, multiplied with the constant 0.659 to reproduce the empirical canopy-height-relationship (K. Meyer, unpublished data), to the height of the shrub. We do not model aboveground competition explicitly because in semi-arid savannas, belowground competition for water is of much greater importance than aboveground competition for light (Wilson 1988; Scholes & Archer 1997; Vila 1997).

Root regrowth proceeds cell by cell in an iteration over all roots of a shrub nested within an iteration over all shrubs whose order is randomized. At the end of each growth step, the remaining regrowth length *L* is updated for every root by subtracting the distance covered (one side or diagonal length of a cell, see below). The iteration excludes roots that have stopped to grow or that have a remaining regrowth length of 0. To be able to process root growth even if the remaining regrowth length is less than one cell, we apply a probabilistic procedure based on the ratio *r* of the remaining regrowth length and cell size. The probability for a root to be admitted to another growth step is proportional to *r*. Both the side length of a cell *S* and the diagonal length of a cell *D* have to be included in *r*, because root growth can proceed in cardinal or intermediate direction (see below), *i.e.* $r(L) = 0.5*(L/D + L/S)$. For every root, $r(L)$ is calculated. If $0 < r \leq 1$, root growth proceeds for another step with probability *r*. If another growth step does

not occur, the remaining regrowth length is set to 0. Otherwise, the next cell to be grown into can be determined.

The most distant cell of the root has the choice between three cells for its next growth step depending on its original growth direction (cardinal or intermediate). These are the three closest cells to the original growing direction if we imagine the most distant cell of the root to be the starting cell of the root (see A, B, and C in Fig. 5.1). The cell among the three cells of choice which has the shortest linear distance to the original growing direction (A in Fig. 5.1) has *line probability* (Table 5.1) to be grown into. The other two cells have a probability of $b/(b+c)$*(1-*line probability*) and $c/(b+c)$*(1-*line probability*), respectively, with b and c representing the respective perpendicular distance of the cell to the original growing direction in units of cells.

Before a chosen cell can be occupied by a root, the prospective uptake zone around the chosen cell is searched for the existence of uptake zones of competing roots. In case of an overlap of two uptake zones, one of seven mutually exclusive competition scenarios applies:

1. Both roots stop to grow (and are assumed to turn vertically downwards as observed at the field site).
2. Both roots stop to grow and the respective opposite roots compensate for the remaining root growth length.
3. One randomly selected root stops to grow (and turns downwards).
4. The randomly selected root stops to grow and its opposite root compensates.
5. Asymmetric competition: The root belonging to the shrub with the smaller canopy diameter stops to grow (and turns downwards).
6. Asymmetric competition: The root belonging to the shrub with the smaller canopy diameter stops to grow and the opposite root compensates.
7. Nothing happens, complete overlap of uptake zones is allowed (which was observed several times during root excavations at the field site).

If competition does not lead to the growth stop of the root, it occupies the chosen cell and its remaining regrowth length is reduced according to the direction of growth (growth in cardinal direction covers less distance than growth in intermediate directions). We apply toroidal edge correction if root growth exceeds the borders of the grid. For every shrub, maximum root system radius and age are updated after the end of all growth steps.

Grass growth. – Grass canopy diameter growth is deterministically set to 5 cm per year (Table 5.1) because no field data are available on individual regrowth length and its relation to soil moisture or tuft size. Grass age and the uptake zone of the grass are updated corresponding to canopy growth.

III. Model calibration and validation

For calibration and validation of SATCHMO, the model was run 10 times with the default parameterization (Table 5.1). We calculated the standard error of the average shrub cover over time of 10 simulations. We use shrub cover as the main output variable because it is directly related to shrub encroachment. However, when we use shrub cover in the following, the result applies to shrub population sizes as well because shrub cover and population size are strongly correlated (Pearson's correlation coefficient: 0.99).

We determined the maximum and minimum shrub cover of 10 simulations to compare it with literature values (Sankaran *et al*. 2005). For model calibration, the simulated and observed average annual shoot regrowth lengths were compared with *t*-tests. The simulated regrowth length was determined as the slope of the linear relationship between canopy diameter and age of all shrubs older than one year within 500 years. The observed regrowth length was obtained from averaging over all regrowth length measurements of 282 shrubs in 2004 and 2005 including non-regrowing shrubs with a zero. For model validation, emergent properties of SATCHMO such as average population sizes, maximum canopy diameter, and shrub thicket diameter were compared with the respective field data. Population sizes were compared with *t*-tests. Simulated population size in the model grid (50 m × 50 m) includes only shrubs older than one year and was averaged over 500 years. Observed population size was averaged over ten 10 m × 10 m plots and 20 15 m × 15 m plots and converted to model grid dimensions. The maximum canopy diameter and the size-frequency distributions of all shrubs occurring during 10 runs of 500 simulation years and of 461 observed shrubs in 2004 and 2005 were visually compared. For the simulation year with the maximum canopy diameter, we determined the diameter of the simulated shrub thickets via the spatial distribution of their canopies based on a Neyman-Scott clustering process as described in Chapter 4 for the top left 15 m × 15 m corner of the model grid. Following the same procedure, we determined the observed shrub thicket diameters for 20 15 m × 15 m field plots and compared the averaged values with *t*-

tests. All *t*-tests were applied with Welch-correction to account for unequal variances. All statistical analyses were carried out with the software package R.

IV. Sensitivity analysis

We applied the global sensitivity analysis method Latin Hypercube sampling to save processing time while covering as much parameter space as possible (McKay *et al.* 1979). We included 27 parameters in the analysis and chose the ranges and distributions for the sampling procedure according to best knowledge or field data distributions if available (Table 5.1). For each parameter, 11 values covering the whole range of the parameter were specified and reordered randomly generating 10 input parameter sets. This procedure was replicated three times. The model was run 10 times for each set of parameters. In six cases, the model was run less than 10 times due to processing power constraints, i.e. 3, 1, 5, 3, 8, and 6 times. Additionally, two simulation runs were excluded from the analysis because the shrub population went extinct within the first 300 years of pre-simulation. The resulting shrub cover and population sizes were averaged over time and over the simulation runs. After a successful check of normality and independence of errors, two linear regression models were applied with shrub cover and population size, respectively, as response variables and the 27 parameters as explanatory variables. During regression model simplification, the least significant parameters were excluded stepwise from the analysis until the model contained only significant parameters ($p < 0.05$). To obtain a measure for the relative importance of the remaining parameters with respect to shrub cover and population sizes, the standardized regression coefficients were calculated as the absolute ratio of the coefficient and the corresponding standard error.

Results

Model validation

The standard error of the average shrub cover and of the average population size over 10 runs is very low (cover mean ± S.E.: 16.80% ± 0.14%, population size mean ± S.E.: 794 ± 9). Simulated maximum and minimum cover of 31.11% and 6.51% agree well with maximum and minimum cover of 38.58% and 0% predicted for a mean annual precipitation of 377 mm by the relationship found by Sankaran *et al.* (2005). Average annual shoot regrowth length, average population size, and average thicket diameter are not significantly different for simulated and observed shrubs (Table 5.2).

Table 5.2: Simulated (1-10) and observed (Obs.) average annual regrowth length, population size, maximum canopy diameter and shrub thicket diameter. †

	Annual regrowth length (cm)	Population size	Maximum canopy diameter (cm)	Year	Thicket diameter (cm)
1	3.07	537	434	300	182.4
2	3.08	509	457	310	268.4
3	3.06	531	445	302	192.4
4	3.01	528	455	730	175.2
5	3.10	519	402	410	124.0
6	3.06	558	481	385	164.4
7	3.10	527	387	380	200.8
8	3.09	513	550	655	124.0
9	2.94	524	416	610	174.4
10	3.08	522	398	340	207.2
Obs.	3.38	584	560	2004	178.4
t	1.656	-0.586	-	-	-0.055
df	284.235	29.114	-	-	21.455
p	0.10	0.56	-	-	0.96

† Simulations are based on the default parameterization and were run ten times. Simulated average *annual regrowth length* was determined as the slope of the linear relationship between canopy diameter and age of all shrubs older than one year within 500 years. The observed regrowth length was obtained from averaging over all regrowth length measurements of 282 shrubs in 2004 and 2005 including non-regrowing shrubs. Simulated *population size* in the model grid (50 m × 50 m) includes only shrubs older than one year and was averaged over 500 years. Observed population size was averaged over ten 10 m × 10 m plots and 20 15 m × 15 m plots and converted to model grid dimensions. *Maximum canopy diameter* was determined from 500 years of simulation, and from two years of observation of 461 shrubs. *Year* gives the year when the maximum canopy diameter occurred. For this year, the shrub *thicket diameter* was determined as 2σ based on a Neyman-Scott clustering process (for details see Chapter 4) for the top left 15 m × 15 m corner of the model grid and for 20 15 m × 15 m field plots (here, the average is shown). Observed and simulated average values were compared with *t*-tests with Welch-correction for unequal variances (*t* - test statistic, *df* – degrees of freedom, *p* – *p*-value).

The observed maximum canopy diameter of 560 cm is very closely reached by the simulated maximum canopy diameter of 550 cm (run 8 in Table 5.2). Visual comparison of the simulated and observed size-frequency-distributions of canopy diameters reveals fairly good agreement (Fig. 5.4).

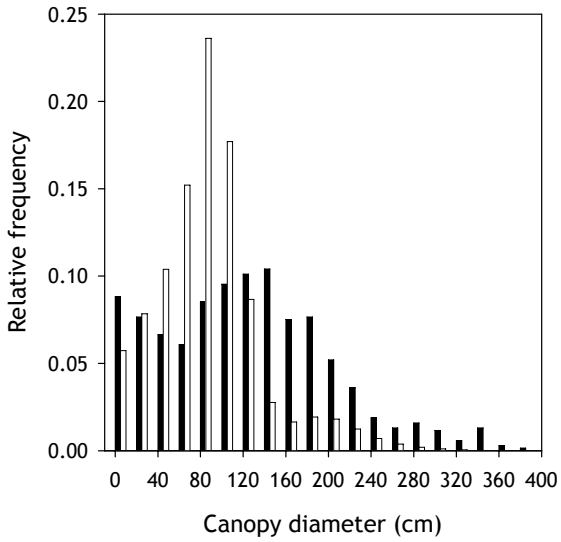

Fig. 5.4: Distribution of relative frequencies of the canopy diameter of 461 observed shrubs (solid bars) and all simulated shrubs occurring during 10 runs of 500 simulation years (open bars). The representation of the distribution is truncated at 400 cm because relative frequencies would not have been visible (total remaining frequencies: observed - 0.0014, simulated - 0.00003).

Sensitivity analysis

The number and identity of significant parameters in the minimum adequate model of the sensitivity analysis results was similar for the response variables shrub cover (9 out of 27 parameters sensitive) and population size (11 sensitive parameters). In both cases, most of the demographic parameters such as mortality of established shrubs and shrub germination rate were eliminated from the final model, as well as environmental variables such as fire frequency and soil porosity (Table 5.1). For shrub cover, the cumulative seed moisture threshold was the most important parameter, followed by soil depth, browsing mortality of seedlings, grass mortality, interception of shrub canopies, germination moisture of grasses, relative water uptake, mean rainfall, and soil field capacity (Table 5.1). With the exception of mean rainfall, the same parameters were retained in the population size-analysis, albeit in a different order and supplemented by the parameters critical soil moisture of shrubs, maximum evapotranspiration, and seedling mortality coefficient (Table 5.1). Population size is by far most sensitive to browsing mortality of seedlings (Table 5.1).

Discussion

The spatially-explicit, individual-based simulation model SATCHMO was built to investigate the small-scale conditions leading to cyclical successions within savanna patches. The successful validation of emergent properties of SATCHMO such as maximum canopy diameter, population size, and shrub thicket diameter shows that SATCHMO is suitable for studying the small-scale shrub cover and population size dynamics in a semi-arid savanna. The agreement between model and data collected at the field site is enhanced by successful comparisons of minimum and maximum shrub cover from simulations with the respective values derived from the empirical relationship found by Sankaran *et al*. (2005) in their comprehensive study of more than 800 data points from African savannas. For a savanna with more rain than at our field site (675 mm vs. 377 mm mean annual rainfall), the maximum equilibrium shrub cover (40%, Roques *et al*. 2001) was also slightly higher than the maximum cover in our simulated semi-arid savanna patch (31%). Hence, SATCHMO can be used to generate realistic conclusions of a semi-arid savanna in general which are not restricted to the shrub population and cover dynamics at our field site. Specifically, SATCHMO can be used to mechanistically explore the ecological processes that produce the patterns found in semi-arid savannas, such as the relationships discovered by Sankaran *et al*. (2005). The hypothesis that one such mechanism may be patch-dynamics can be tested with SATCHMO by searching for positive autocorrelation in the simulated shrub cover time series.

The sensitivity analysis of SATCHMO quantitatively confirms the common view that soil moisture is the most important parameter affecting shrub cover dynamics in semi-arid savannas (Sankaran *et al*. 2005). Still, it is surprising that almost none of the demographical parameters such as shrub germination probability or shrub mortality is of importance for shrub cover dynamics, leading to the conclusion that demographic bottlenecks inherent to the population (as described by Sankaran *et al*. (2004) do not matter as much as external factors. With respect to model structure, this can be explained by soil moisture being the key driver of processes in SATCHMO. While shrub and grass growth, competition, mortality, and reproduction depend on soil moisture, there is only a weak indirect feedback of these processes to soil moisture (*e.g.*, via uptake zones depleting the available water in the cells they cover and by canopies intercepting precipitation). Thus, without sufficient soil moisture, shrub growth and reproduction are impaired and mortality increased, generating high sensitivities of shrub cover and population sizes to soil moisture parameters. This is particularly apparent when focussing on

the most sensitive parameter with respect to shrub cover: The cumulative moisture threshold for seed production is invoked early in the annual cycle of population dynamics and its high sensitivity points to the importance of seed production conditions – without seeds no adult shrubs can grow. This is in agreement with the patch-dynamics concept where years of overlapping local rainfall events may create the necessary conditions for mass recruitment and subsequent expansion of whole shrub cohorts leading to the naturally encroached phase of the successional cycle (Wiegand *et al.* 2006). The only sensitive parameter related to shrub demography is browsing mortality of shrub seedlings. Analogous to the soil moisture parameters, seedling mortality occurs early in the life cycle and therefore creates the conditions subsequent demographic processes such as growth rely on.

However, the majority of the sensitive parameters are not well studied, *e.g.*, browsing mortality of seedlings or relative water uptake (see Accuracy in Table 5.1). In the light of increasing shrub encroachment, it would be valuable to invest more effort into the empirical study of these parameters in the future because these parameters are of major importance for the determination of shrub cover. Management will be efficient if centered on sensitive parameters that are easy to manipulate. If management aims at reducing shrub encroachment, continuous action would be required in a patch-dynamic savanna because cyclical succession has to be stopped at the desired shrub density and further succession has to be prevented. Moreover, the sensitive parameters identified in the present study are not easy to manipulate, because holding the cycle in the phase dominated by grass would require reducing soil moisture parameters. The only exception may be browsing mortality of seedlings which could be raised with a reasonable effort. In particular, following our results, fire management may not be efficient in arid and semi-arid savannas because fire frequency was one of the first parameters eliminated from the regression model during model simplification. This agrees with the common notion that fire does not play an important role in arid savannas where precipitation is not sufficient to allow for enough grass biomass to fuel frequent and intense fires (Bond & Van Wilgen 1996; Higgins *et al.* 2000; Bond *et al.* 2003).

Sankaran *et al.* (2004) split savanna models into two families: competition-based models and demographic-bottleneck models. Competition-based models concentrate on spatial or temporal concentration of intra- versus inter-specific competition and mostly ignore life-stage dependency of competition although there is evidence for it (Scholes & Archer 1997; House *et al.* 2003). On the other hand,

most demographic bottleneck models do not include competitive interactions explicitly or only semi-quantitatively (Sankaran *et al*. 2004). Hence, for a better understanding of savanna dynamics, Sankaran *et al*. (2004) advocate new savanna modelling approaches taking explicitly into account demographic bottlenecks and competitive interactions at each life stage of a shrub. This claim is based on the rationale that coexistence may be reached if intra-life form competition is stronger during periods favourable for that life form and inter-life form competition otherwise (Chesson & Huntly 1997, Chesson 2000). Following Sankaran *et al*.'s (2004) suggestion, we constructed SATCHMO as a demographic-bottleneck model that explicitly includes different competition scenarios between shrub roots as well as competition for water in cells that are covered by the uptake zones of more than one individual grass or shrub. Competition is life-stage dependent because small shrub seedlings have much smaller uptake zones than established shrubs and also than most grass tufts. This results in strong competition when a seed is dispersed to a location completely covered by a larger uptake zone of another individual. As the soil moisture taken up within the uptake zones is translated quantitatively into regrowth length, competition is included quantitatively as it was called for by Sankaran *et al*. (2004). During periods favourable for shrubs, shrub densities and uptake zones expand, leading to greater probabilities of intra-life form contact and subsequent intra-life form competition. Hence, SATCHMO unifies the competition-based approaches with the demographic-bottleneck ideas by placing a strong focus on spatially explicit belowground interactions.

In the future, further applications of SATCHMO may include the explicit investigation of patch-dynamics by the identification of cycles in shrub cover dynamics over time and their relationship to annual precipitation and other savanna determinants. SATCHMO is also well suited to comparing the consequences of different belowground competition scenarios for savanna dynamics in general and shrub encroachment in particular at a great level of detail which would be much more time-comsuming in the field. This could be supported by the analysis of the spatial patterns of long-term chronosequences of model shrubs and grasses. Patterns emerging under the competition scenarios (i.e. symmetric/ asymmetric, with/ without compensation, no competition at all) can be tested for agreement with field patterns. Only those scenarios that result in equivalent patterns may have acted in nature. This way one could screen the competition scenarios for fulling the hypothesis that the long-term impact of competition leads to less aggregated spatial shrub patterns (Wolf 2005).

Among the strengths of SATCHMO is the explicit and detailed simulation of belowground growth and competition matching the recognized importance of belowground interactions in savannas (Scholes & Archer 1997). SATCHMO is based on a solid field data foundation and has been successfully validated with independent field data for a semi-arid savanna. SATCHMO operates on large temporal scales allowing the evaluation of long-term spatially explicit savanna woody species dynamics.

Admittedly, the great level of spatial and temporal detail comes at a cost because the processing of certain scenarios can be quite computing-power-intensive. Fortunately, the small standard errors justify a reduced number of simulations, although more replications are of course always desirable as they increase the power of the conclusions. Another drawback of the model is its small spatial scale which serves the current purpose of investigations but should be expanded to the landscape-scale to be able to ultimately test the predictions of the patch-dynamics concept and its integrative power. To keep SATCHMO as simple as possible in spite of the high level of detail desired, some aspects of reality were not included that were not necessary to fulfil the current purpose of SATCHMO. If the model purpose was expanded to focus more on grass population dynamics and given the availability of the relevant field data, it could be reasonable to also include an explicit feedback of soil moisture on grass growth and explicit competition scenarios between grasses and shrubs. Possible extensions to belowground growth and interactions could be active root foraging behaviour according to moisture gradients in the root neighbourhood and the implementation of facilitative interactions or mixed competition scenarios. In mixed competition scenarios, the type of competitive interaction could depend on the actual conditions, *e.g.*, root overlap without consequences prevails in years with high precipitation and asymmetric competition with strong territoriality (=wide uptake zones) in drought years.

Additionally, SATCHMO can be easily extended to include an overgrazing scenario to test the relative importance of natural drivers of shrub encroachment and overgrazing. To increase reality of the model, shrub objects with the characteristics of other important savanna woody species may be added to investigate tree-tree-interactions and their positive and negative feedbacks influencing overall woody species densities and encroachment. Management or encroachment restoration scenarios can easily be included and tested with SATCHMO by evaluation of the consequences for long-term shrub dynamics, *e.g.*,

Smit's (2004) hypothesis that thinning of woody species to small densities of large individuals will prevent shrub encroachment most effectively. After a scaling-up procedure, generalized results on patch transition frequencies and duration of transitional states (woody, grassy, bare ground) from SATCHMO can be used to parameterize a patch-dynamic landscape-scale model. If the landscape-scale population dynamics and spatial patterns of woody species correspond to those derived from aerial photographs from corresponding semi-arid savannas, the patch-dynamics concept has the potential to be one integrative mechanism explaining tree-grass coexistence and shrub encroachment in savannas.

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Appendix A

Algorithm for the calculation of soil moisture for a specific cell with residual soil moisture from the previous day $s(t\text{-}1)$ based on Rodriguez-Iturbe *et al.* (1999):

1. Given rainfall $R(t)$, calculate soil moisture $s'(t)$ including interception $D(t)$, but not yet considering evapotranspiration and leakage:

   If $R(t)>0$ $\quad s'(t) = s(t\text{-}1) + R(t)\ /nZ - D(t)\ /nZ$

   Else $\quad s'(t) = s(t\text{-}1)$

2. Calculate evapotranspiration $E(s'(t),t)$ taking critical soil moisture s_c and maximum evapotranspiration E_{max} into account where s_c defines the threshold when plants begin closing their stomata:

   If $s'(t) \geq s_c$ $\quad E(s'(t),t) = E_{max}$

   Else $\quad E(s'(t),t) = (E_{max}/\ s_c)^*\ s'(t)$

3. Calculate leakage $L(s(t),t)$ including soil field capacity s_{fc}:

   If $s'(t) > s_{fc}$ $\quad L(s(t),t) = s'(t) - s_{fc}$

   Else $\quad L(s(t),t) = 0$

4. Update soil moisture:

   $$s(t) = s'(t) - E(s'(t),t)\ /nZ - L(s(t),t).$$

Appendix B

Fitting procedure for the relationship between moisture and regrowth based on approximations from field data: With

Moisture = a*shoot growth + b*canopy diameter + c*seeds + d*root growth + e, (B1)

Root growth = f*shoot growth + g, (B2)

Shoot growth = (moisture$^{-0.5}$ – b*canopy diameter - c*seeds – e – d*g) / (a + d*f), (B3)

where a to g are regression coefficients which were estimated from field data. Unfortunately, there was no data set available encompassing values for all these variables at the same time, and for soil moisture, no direct measurements were accessible. However, approximations were possible based on the field data that were available. The largest available data set comprised canopy diameter, height, and shoot regrowth length (but not seed number and root regrowth length) for 590 *A. mellifera* shrubs in 2004 and 2005.

To obtain an estimate of seed number, we calculated the number of seeds for all heights in the data set from equation (2). For an estimate of root regrowth length, we assumed that the relation of root regrowth length to root length is the same as the relation of shoot regrowth length to canopy radius. From quantile regressions, we know that canopy diameter is significantly related to maximum root length (Meyer *et al.* 2005). Hence, we estimated root length as a random value between the 0.5- and the 0.9-regression quantile at the given canopy diameter in the data set. With root length, shoot regrowth length, and canopy radius, we estimated root regrowth for the data set.

To determine the moisture uptake of the shrubs of the data set, the area of the uptake zone of the shrubs was calculated as the sum of eight rectangles. The area of each rectangle was calculated as the product of the root length of the shrub and the width of its uptake zone. Thereby, we assume that the eight roots of a shrub had all the same lengths and had followed their original direction without deviations. The total area of the uptake zone of a shrub was partitioned into the part under bare ground and the part under the shrub canopy.

An absolute annual soil moisture value (in mm) was calculated from the Kimberley weather data for bare ground and shrub canopy-covered ground for 2004 and 2005, respectively. Absolute annual moisture uptake per shrub (in mm^3) was estimated as absolute annual moisture uptake multiplied with the uptake zone areas under bare ground and under the shrub canopy. In this estimation, possible moisture losses due to competitive uptake zone overlap are not included.

6
The rhythm of savanna patch-dynamics

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Abstract

Patch-dynamics is a new, potentially unifying mechanism for the explanation of tree-grass coexistence in savannas. In this scale-explicit paradigm, savannas consist of patches in which a cyclical succession between woody and grassy dominance proceeds spatially asynchronously. The growing ecological and economic problem of shrub encroachment is a natural transient phase in this cycle. An important step towards understanding patterns at the landscape-scale is achieved by investigating mechanisms at a smaller scale. We developed the spatially-explicit individual-based simulation model SATCHMO to test the null-hypothesis that cyclical succession cannot emerge from a realistic patch-scale simulation model of the population dynamics of savanna woody species. We found a significantly positive temporal autocorrelation in shrub cover time series indicating the existence of cycles with a typical duration of about 33 years. The shrub size-frequency distributions over the course of a cycle showed shifts from dominance of small shrub sizes towards larger sizes during the rising phase of a cycle and the reverse in the declining phase. This supports the three-phase explanation of (1) an initial phase when overlapping favourable conditions lead to mass recruitment of shrubs, (2) a build-up phase when the shrub cohort grows simultaneously, and (3) a break-down phase when increased competition due to crowding and unfavourable conditions lead to the break-down of the shrub cohort. The frequency-distribution of shrub age at death over 10 simulations was also in agreement with this explanation. We investigated the relationship between shrub cover, annual precipitation and time-lagged shrub cover to identify the driver of the cyclical successions. More than 90% of the variation in shrub cover was explained by shrub cover of the previous year, precipitation, and their interaction. With the demonstration of precipitation-driven cyclical succession at the patch-scale, we show that the mechanistic, temporal component of patch-dynamics can be used to explain tree-grass coexistence in semi-arid savannas.

Key Words

cyclical succession, *Acacia mellifera*, individual-based simulation model, scale, tree-grass coexistence, shrub encroachment, patch-scale, temporal autocorrelation, size-frequency distributions.

Introduction

Scale is a fundamental conceptual problem in ecology because different processes occur at different scales and are linked to patterns at other (mostly greater) scales (Levin 1992). For a general understanding, ecological theories and empirical studies should therefore not be restricted to one scale. Patch-dynamics is a useful framework to capture ecosystem dynamics spanning several scales of observation. In patch-dynamics, it is assumed that the landscape consists of distinct patches of variable size. In every patch, the same cyclical succession proceeds. The successional states may be of variable duration and occur spatially asynchronously. The proportion of each state will be approximately constant at the landscape-scale. Hence, at large scales, an equilibrium can persist, although at small scales, non-equilibrium dynamics prevail (Levin 1992). Since Watt's (1947) first account of patch-dynamic ecological systems, patch-dynamic modelling frameworks have been developed (Wu & Levin 1997; Levin *et al.* 2001) and the patch-dynamics paradigm has been applied to a multitude of ecosystems, *e.g.*, forests (Remmert 1991), intertidal communities (Levin & Paine 1974; Paine & Levin 1981), grasslands (Coffin & Lauenroth 1990), or aquatic ecosystems (Steele 1978).

However, only recently, the first empirical attempts have been made to explain tree-grass coexistence in savannas with patch-dynamics (Gillson 2004; Wiegand *et al.* 2005; Wiegand *et al.* 2006). Thus far, only scale-free mechanisms have been put forward to explain tree-grass coexistence in savannas. The first and still prominent explanation is the two-layer hypothesis, based on a rooting-depth niche separation between trees and grasses (Walter 1971). However, evidence for this hypothesis to date is equivocal. For example, tree-grass coexistence has been shown on soils too shallow for rooting-depth differentiation (Wiegand *et al.* 2005). Other hypotheses include a storage effect of reproductive potential of woody species over unfavourable periods (Higgins *et al.* 2000), disturbances such as fire acting as buffer that keep both grasses and trees in the system (Scholes & Archer 1997; Jeltsch *et al.* 1998b; Jeltsch *et al.* 2000), or spatially heterogeneous locations that are favourable for either grass or tree establishment (Jeltsch *et al.*

1998a). All mechanisms proposed to date are restricted to certain environmental conditions; a unifying mechanism is lacking. Patch-dynamics have the potential to be this unifying mechanism because it acknowledges the importance of scale and is general enough to allow the integration of most of the mechanisms suggested. In a patch-dynamic savanna, patches cycle between grassy and woody dominance leading to tree-grass coexistence at the landscape-scale. Hence, the patch-dynamics framework integrates the spatial-heterogeneities explanation by Jeltsch *et al.* (1998a). Other hypotheses such as the disturbance explanation (Scholes & Archer 1997; Jeltsch *et al.* 1998b; Jeltsch *et al.* 2000) or the storage effect (Higgins *et al.* 2000) could be integrated as triggers and drivers of the successional cycles.

Understanding savannas as patch-dynamic systems would also have implications for management issues. In a patch-dynamic savanna, the worldwide ecological and economic problem of shrub encroachment, *i.e.*, the increase in density of woody species often unpalatable to lifestock (Smit *et al.* 1996), is only a natural phase during the successional cycle. In the patch-dynamics paradigm, shrub encroachment may be enhanced by overgrazing, as suggested by empirical evidence (Skarpe 1990b, 1990a; Perkins & Thomas 1993), but would be an inherently natural and transient phenomenon.

In order to test the validity of patch-dynamics as an explanation of tree-grass coexistence in savannas, simulation models are an appropriate tool because they can capture the large scales involved more easily than empirical studies (Levin 1992; but see Gillson 2004 for a paleological study spanning different scales). However, an understanding of patterns at larger scales is promoted by investigating mechanisms at the smaller scale (Wu & Loucks 1995). To obtain this small-scale understanding, the spatially-explicit individual-based patch-scale simulation model SATCHMO was developed (see also Chapter 5). Patch-dynamics implies cyclical succession at the patch scale. Thus, in the present study, we want to test the null-hypothesis that cyclical succession cannot emerge from an ecologically realistic patch-scale simulation model of the population dynamics of savanna woody species. If cyclical succession does emerge from SATCHMO, the second aim of this study is to provide a mechanistic explanation for the cycles and to identify the driving factors of the cyclical succession.

Methods

The results presented here are based on the spatially-explicit, individual-based patch-size simulation model SATCHMO which is described in detail in Chapter 5. In

the following, only model features relevant to the present study are summarized. For model details, default parameter values, validation, and sensitivity analysis refer to Chapter 5.

Study area

SATCHMO is based on field data that were collected in semi-arid savanna in the Kalahari thornveld at Pniel Estates (S 28° 35', E 24° 29'), 30 km north of Kimberley, South Africa, between 2003 and 2005 (see also Meyer *et al.* 2005, Chapter 2). Mean annual precipitation is 377 mm and mostly occurs as thunderstorms throughout the summer months (September to March). The multi-stemmed blackthorn (*Acacia mellifera*) is the dominant woody species in the study area.

Model structure and scales

The basic objects in SATCHMO are a shrub, a grass tuft, and the root of a shrub. Until the age of one year, shrubs and grasses are referred to as seedlings, thereafter as established shrubs and grass tufts. Shrubs were modelled following the characteristics of the dominant species in the area, *A. mellifera*. Aboveground, shrubs and grasses older than one year are represented by a circle corresponding to the canopy diameter of the individual. To appreciate the predominant importance of soil moisture mediating plant interactions in semi-arid savannas, we modelled shrub roots spatially explicitly in two dimensions. The shrub root system is represented by eight horizontal roots which initially stretch from the shrub rooting point into the cardinal and intermediate directions. Roots are surrounded by an uptake zone whose width approximates the length of side-roots responsible for water uptake. Grass tufts serve as interspecific competitors for the shrubs. Grass roots were not modelled spatially explicitly because grass was not in the focus of the model and because information on grass roots is scarce. Instead, water uptake occurs in a circular uptake zone around the grass canopy.

SATCHMO is based on a two-dimensional grid with 512 x 512 cells comprising one patch in the patch-dynamics paradigm. The spatial resolution is 10 cm and the spatial extent of the grid corresponds to 51.2 m which is justified by field observations (Chapter 4). The temporal resolution is daily for precipitation and annual for shrub and grass dynamics. The temporal extent of the simulations is 500 years to capture long-term savanna dynamics.

Initialization

Initially, one reproductively-mature shrub is located in the centre of the grid supplemented by ten randomly-arranged grass tufts with initial characteristics corresponding to average field data values. Model evaluation started after 300 years of simulation to exclude an influence of initial conditions (Chapter 5).

Environmental parameters

In semi-arid savannas, water limits plant growth much more than nutrients, and still noticeably more than fire or grazing (Sankaran *et al.* 2005). Hence, among the possible environmental variables, we do not explicitly take nutrient dynamics and grazing into account although they are implicitly included in the field data underlying SATCHMO. We model fire with less detail because in arid and semi-arid savannas, there is not enough grass biomass present to fuel frequent and intense fires. We rather focus on a detailed characterisation of precipitation and soil moisture in SATCHMO. A daily precipitation value is calculated for the model grid according to the Zucchini-algorithm for South-African rainfall (Zucchini *et al.* 1992) based on local weather data. Fire is characterised by its frequency with a maximum of one fire per year and a field data-based default value of 0.006 $year^{-1}$ (Chapter 2, Chapter 5). The occurrence of a fire leads to increased mortalities in established shrubs and especially in shrub seedlings. Shrub growth, grass mortality, and grass growth are not modified by fire due to compensation for biomass losses until the end of the season (Donaldson 1967; Noy-Meir 1995; Van de Vijver *et al.* 1999).

Soil moisture

Soil moisture is the basic currency of the model mediating competition, growth, and some aspects of mortality and reproduction. Soil moisture is calculated independently for each grid cell from the overall precipitation value to account for the influence of roots or canopies on water budgets. Based on Rodriguez-Iturbe *et al.* (1999), temporal relative soil moisture dynamics is obtained from reducing precipitation by water lost through vegetation interception, evapotranspiration, and leakage to lower soil layers divided by soil porosity and soil depth (for details, see Chapter 5). We modelled a soil depth of 70 cm based on data from *A. mellifera* root excavations. Surface runoff is not included because a flat area is modelled where inflow and outflow level out.

Shrub reproduction

In all demographic rates, stochasticity is included. Shrubs can reproduce vegetatively and sexually. However, due to little evidence for vegetative reproduction (Chapter 5), the probability of vegetative reproduction and the numbers of resprouts randomly distributed within the root extent are very low (0.0005 and 15 per reproducing shrub, respectively). Within one year, either all shrubs reproduce vegetatively or all shrubs reproduce sexually (if at all). Seed production occurs in all mature shrubs if a certain threshold of local total cumulative soil moisture between September and November is exceeded. The threshold is estimated from local weather data (Chapter 5). Based on an empirical relationship, maturity is reached with a height of 104 cm and the number of seeds per reproducing shrub is size-dependent (number of seeds = 22.98 height (cm) – 2380, Chapter 5). Seed dispersal includes aggregated short-distance dispersal within the canopy of the mother shrub (60% of the seeds) and twice the canopy radius (35%) and random long-distance dispersal in the whole grid (5%, Chapter 5). To account for intraspecific competition, only one seed per cell (100 cm^2) is allowed. When seed location would be outside the grid borders, toroidal edge correction is applied, *i.e.* seeds leaving the grids on one side enter the grid on the opposite side. Germination of shrub seedlings is contingent on soil moisture reaching a cell-specific cumulative soil moisture threshold during a certain number of successive days which were determined from local weather data. The field data-based germination rate is 0.19 (Chapter 5).

Shrub mortality

The basic seedling mortality depends on the soil moisture in the cell where the seedling is located. The respective seedling mortality coefficient was estimated from a field experiment (seedling mortality = $75.95*10^{6\,(-\text{soil moisture})}$, Chapter 5). This basic seedling mortality is supplemented by a high natural browsing mortality (0.95) to account for the strong influence of herbivory on vulnerable seedlings and by an extra fire mortality (0.65). Mortality of established shrubs occurs on the basis of negative regrowth (see section *Shrub growth*), through fire (0.09, Meyer *et al.* 2005) and droughts (0.05). A drought year is a year with less than the long-term mean annual precipitation reduced by one standard deviation. Drought mortality also includes mortality due to browsing because browsing of *A. mellifera* usually occurs in dry periods.

Grass reproduction and mortality

The grass module is based on literature data that was adapted to our field site conditions via the mean annual precipitation. We do not differentiate between sexual and vegetative reproduction because grasses with stoloniferous or rhizomatous growth do not necessarily produce fewer seeds than seed-producing grasses (O'Connor & Pickett 1992), and we focus here on perennials. When the reproduction soil moisture threshold is reached, a fixed density of new grass tufts (2.35 m^{-2}, O'Connor 1994) is distributed randomly over the whole grid. The reproduction soil moisture threshold follows the same conditions as the germination moisture threshold of shrubs including the number of days that are needed for germination. Grass seedling mortality (0.28, O'Connor 1994) applies to all new grass tufts, whereas grass tuft mortality (0.47, O'Connor & Everson 1998) is applied to all tufts older than one year.

Shrub growth

To model the growth of their first two years, new shrub seedlings (age 0 and 1) are deterministically initialized with eight roots with a width of one cell and alternate cardinal and intermediate original growing direction. Roots are surrounded by an uptake zone with a width of 2 cells (corresponding to 20 cm) as a proxy for fine roots where water uptake occurs. The initial canopy diameter is determined from an empirical relationship between root length and shrub size (Meyer *et al.* 2005). For all shrubs older than one year, individual water uptake is calculated by distributing the extractable proportion of the absolute soil moisture (in mm) in each cell at equal parts to all shrubs and grasses whose uptake zones cover the cell.

Whether the amount of water taken up by a shrub is converted into regrowth is specified by the regrowth probability (0.55, Chapter 5). Regrowth length is determined following the rationale that the resources taken up (represented by moisture) have to be used for maintenance of the plant body (canopy diameter), reproduction (seed number), and above- and belowground growth (regrowth length). Based on approximations from field data, we fitted linear models with square-root transformed moisture for seed-producing shrubs and for shrubs without seed production (see Chapter 5 for a detailed account of the fitting procedure and coefficients). Negative regrowth lengths lead to shrub mortality, but only after a buffer is added to regrowth length. This buffer accounts for the competitive effects that were not included into the moisture calculations

and ensures that the emergent mortality of established shrubs matches the empirically determined mortality (see Chapter 5 for the detailed procedure). For shoot growth, regrowth length is added to the canopy radius of the shrub and also to the height of the shrub after multiplication with the constant 0.659 to reproduce the empirical canopy-height-relationship (Meyer *et al.* unpublished data).

Root regrowth proceeds cell by cell in an iteration over all roots of a shrub nested in a randomized iteration over all shrubs. The iteration excludes roots that have stopped to grow, or that have a remaining regrowth length of less than one cell and do not pass a probability threshold (Chapter 5). Growth of individual roots proceeds by a weighted random walk where the greatest probability for the next growth step is assigned to the cell closest to the original growing direction (Chapter 5). Before a cell can be occupied by a root, overlap of the prospective uptake zone with other shrub uptake zones is checked. In case of overlap, the root belonging to the shrub with the smaller canopy diameter stops to grow (asymmetric competition). If competition does not lead to the growth stop of the root, it occupies the chosen cell. We apply toroidal edge correction if root growth exceeds the borders of the grid. For every shrub, age is updated after the end of all growth steps.

Grass growth

Grass canopy diameter growth is deterministically set to 5 cm per year (O'Connor & Everson 1998) because no field data are available on individual regrowth length and its relation to soil moisture or tuft size. Grass age and the uptake zone of the grass are updated corresponding to canopy growth.

Simulation experiments

It is important to note that we define cyclical succession as a cycle between woody and grassy dominance. Hence, shrubs do not necessarily have to go extinct at any point during a cycle. We calculated partial Pearson's autocorrelation coefficients of shrub cover separately for each of 100 simulations with default parameter values for time lags 1 to 200 to determine the existence and period of the successional cycles of shrub cover (see also Venables & Ripley 2003). Significantly positive autocorrelation indicates cyclical behaviour. We allowed for small variations in the frequency of years favourable for shrub cohort build-up and break-down by assessing a moving window of 3 years width along the time lags. Significance of positive (negative) partial autocorrelation was achieved if the window at a certain

time lag contained at least one positive (negative) partial autocorrelation coefficient in at least 95% of the simulations. In the following, a particular moving window of time lags will be referenced only by its central time lag to simplify the presentation.

To be able to compare the period of cyclical successions with maximum shrub age, we determined the frequency distributions and the average, median, and maximum age at death for all shrubs occurring in 10 simulations. To further assess the hypothesis of mass recruitment and subsequent shrub cohort build-up and break-down, we also assembled frequency distributions of shrub canopy diameters from four years sampled from a typical shrub cover cycle during a simulation with default parameter values.

We investigated the relationship between annual precipitation, shrub cover, and lagged shrub cover from 100 simulations with a simple linear model because the diagnostic plots fit well. We included lagged shrub cover to account for temporal autocorrelation. We included shrub cover with time lags of up to seven years because cross-correlation between annual precipitation and shrub cover had revealed significant autocorrelation at time lags of up to seven years. For the visual comparison of precipitation and simulated shrub cover over time, shrub cover was smoothed with robust locally weighted regression with a smoother span of 10 years (Lowess algorithm, Cleveland 1981). All statistical analyses were carried out with the software package R.

Results

Shrub cover was cycling over time with considerable variation in the local maxima and minima (Fig. 6.1). In most cases, the rise of shrub cover values was slow whereas the slope of decreasing shrub cover was steep (Fig. 6.1).

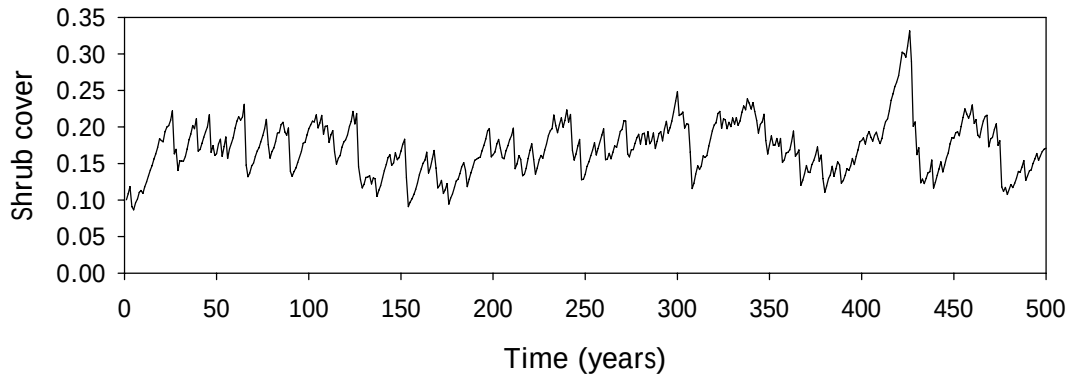

Fig. 6.1: An example simulation run of shrub cover dynamics over time. Shrub cover was measured as the proportion of cells in the model grid covered by the canopy of one or more shrubs.

We a found significantly positive autocorrelation in shrub cover over time at the time lags 2 and 33 years (Fig. 6.2). A negative autocorrelation was significant at 15 time lags ranging from 3 to 189 years (Fig. 6.2).

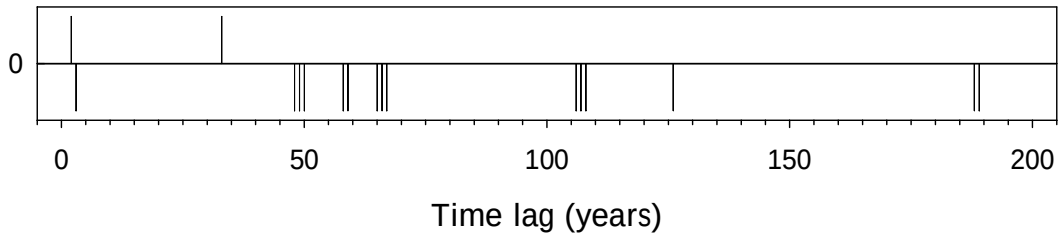

Fig. 6.2: Time lags at which significant positive (bars above the axis) and negative (bars below the axis) partial autocorrelation of shrub cover occurs for 100 simulations over 500 years. A positive (negative) time lag representing the centre of a moving window of 3 years width is significant, if more than 95% of the simulations showed a positive (negative) partial autocorrelation coefficient at at least one of the three time lags covered by the moving window.

Frequency-distributions of shrub age at death were bimodal (Fig. 6.3). The first mode corresponded to high mortality in early stages of growth (up to 5 years). We assumed that these young shrubs did not contribute noticeably to the overall cover of a plot. Because we wanted to compare age at death with the duration of shrub cover cycles, we therefore calculated mean, median, and maximum shrub age at death without shrubs younger than 6 years. The average and median shrub age at death were 40.5 and 40 years, respectively, which approximately matched the values of the second window of significantly positive time lags. Maximum age at death over all simulations and shrubs was 103 years.

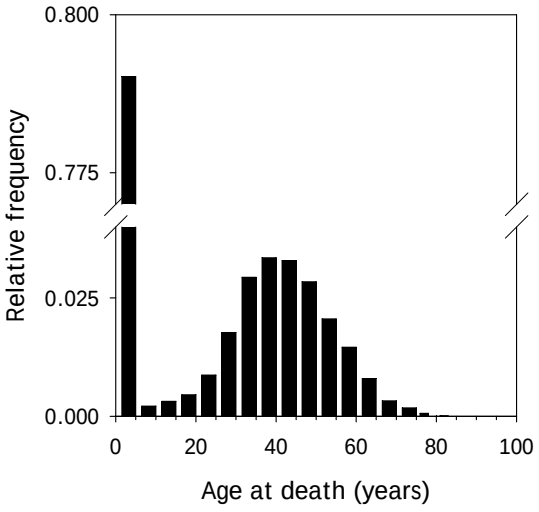

Fig. 6.3: Distribution of relative frequencies of age at death of all shrubs that survived their first year in 10 simulations over 500 years.

With increasing shrub cover, size-frequency distributions of the simulated shrubs shifted from dominance of small shrubs to dominance of larger shrubs (Fig. 6.4a, b). In the declining phase of a shrub cover cycle, the relative frequency of larger shrubs decreased and smaller shrubs dominated again (Fig. 6.4c).

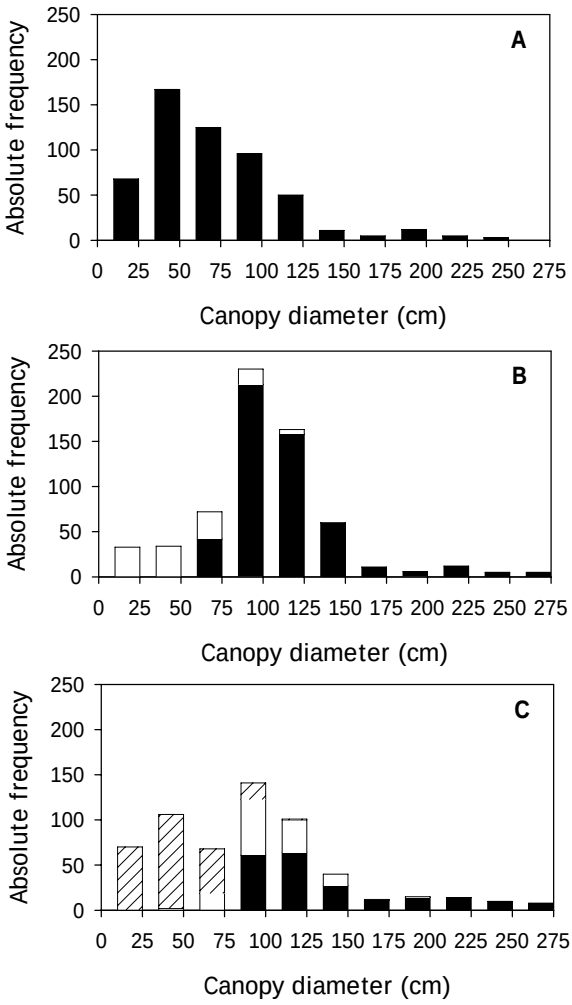

Fig. 6.4: Absolute frequencies of canopy diameters of all simulated shrubs in three simulation years chosen from one exemplary cycle representing the initiation phase (A), the build-up phase (B), and the break-down phase (C). The cycle duration was 32 years. Shrubs with a canopy diameter of less than 6.2 cm were excluded from the analysis. Solid bars represent the shrub cohort present in year A, empty bars represent all shrubs present in year B, but not in A, and hatched bars represent the shrubs present in year C that were not part of the previous shrub cohorts.

Decreasing annual precipitation coincided with decreasing shrub cover over time, especially during drought years (when precipitation falls below the dashed drought line in Fig. 6.5). The minimum adequate model for the prediction of current shrub cover included only the explanatory variables: shrub cover lagged by one year, mean precipitation of the current year, and their interaction ($r^2 = 0.92$). Current cover was positively correlated with rainfall and with shrub cover in the previous year (Fig. 6.6). The greater the cover in the previous year, the steeper was the slope of the positive relationship between rainfall and cover of the current year (Fig. 6.6).

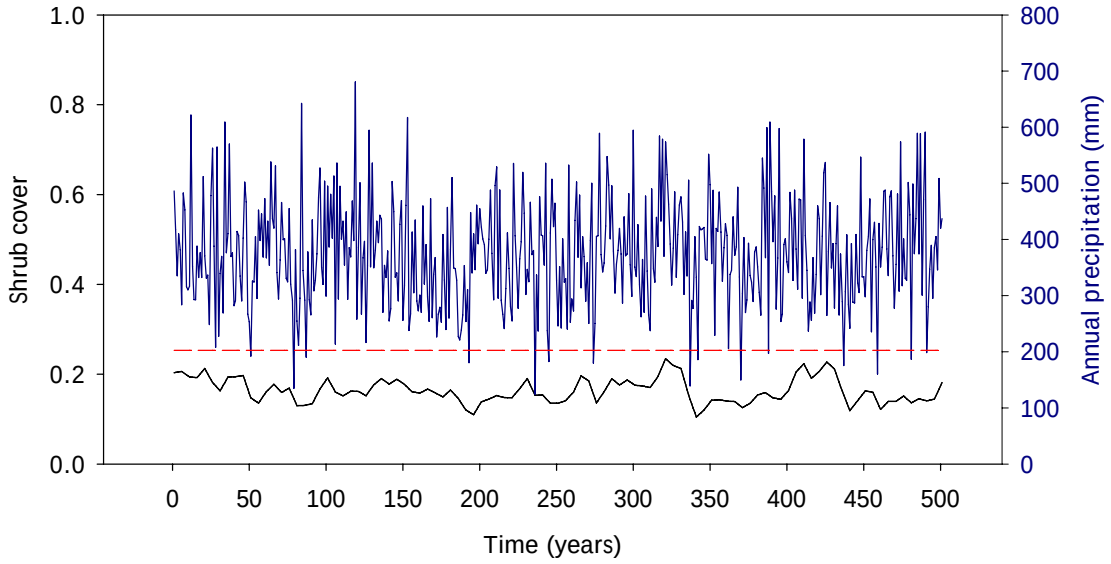

Fig. 6.5: Annual precipitation (blue line) and smoothed shrub cover (black line) over time simulated with default parameter values. Shrub cover was smoothed with robust locally weighted regression with a smoother span of 10 years. In SATCHMO, additional drought mortalities apply if annual precipitation falls under the drought threshold (dashed red line).

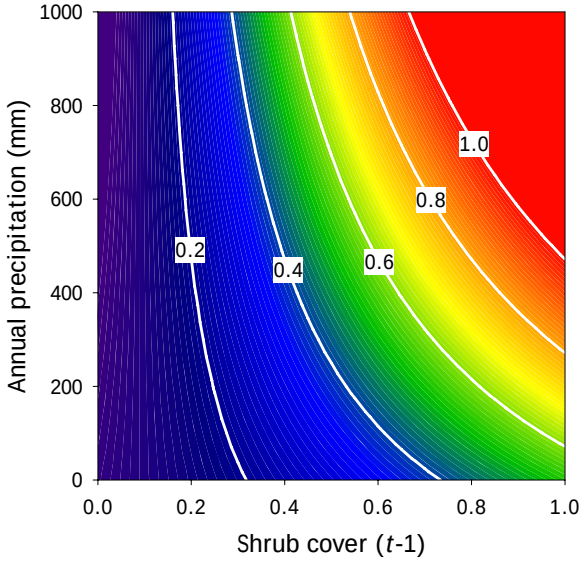

Fig. 6.6: Relationship between shrub cover at time step *t* (contours), annual precipitation, and shrub cover at time step *t*-1 predicted by a linear multiple regression model based on 100 simulations over 500 years (R^2 = 0.92). Regression equation: Shrub cover (*t*) = 0.0472 - 0.0001 * annual precipitation + 0.4811 * shrub cover (*t*-1) + 0.0011 * annual precipitation * shrub cover (*t*-1). All coefficients were significant at $p < 0.001$.

Discussion

In the present simulation study, we provide evidence for cyclical succession of shrub cover in a semi-arid savanna based on the savanna model SATCHMO. We propose the following mechanistic explanation for the shrub cover cycles: (1) In years of locally overlapping favourable environmental conditions, mass germination of shrub seedlings occur (initiation phase). This is also consistent with empirical findings from an arid savanna gradient in Namibia (Wiegand *et al.* 2005). (2) Subsequently, the shrub cohort grows simultaneously as long as environmental conditions do not become too unfavourable (build-up phase). Competition is intensifying. If additional favourable years occur during this phase, additional mass germination events followed by build-up of additional shrub cohorts may contribute to increasing competitive pressure. The build-up phase corresponds to the "upgrade series" in Watt's (1947) description of patch dynamics. (3) If a year with unfavourable environmental conditions coincides with high shrub cover, the shrub cohorts catastrophically break down (break-down phase, corresponding to the "downgrade series" in Watt (1947). The more unfavourable the environmental conditions are, the more likely is a shrub cohort break down already at lower shrub cover. In this phase, large shrubs are more likely to be affected by mortality because their resource needs are greater.

The results of the present study support this three-phase explanation of the shrub cover cycles. Overall, it is intriguing how well the mean age at death of the simulated shrubs (40 years) and the duration of the cycles (33 years) match. Hence, a typical shrub will germinate at the beginning of a cycle and die at the end of a cycle. Specifically, the age-at-death distributions show that the first 5 years present a serious bottleneck in the life of a shrub (Fig. 6.3). This is in agreement with many other studies that identify the seedling establishment stage as the often most limiting stage in the life history of (savanna) woody plants (*e.g.*, Grubb 1977; Chesson *et al.* 2004; Sankaran *et al.* 2004). It can be assumed that locally overlapping favourable conditions for reproduction and early survival will temporarily widen the bottleneck and may lead to mass recruitment of woody species (initiation phase).

Simultaneous growth in the build-up phase is supported by the shift of the mode in the size-frequency distributions towards greater sizes in this phase (Fig. 6.4b). The series of size-frequency distributions assembled from simulations agrees very well with the one postulated by Wiegand *et al.* (2005) for a patch-dyanmic savanna. The slow increase of shrub cover compared to its steep decline

during the cycles emerging from simulations provides evidence for additional shrub cohorts joining in during the build-up phase (see also different signatures in Fig. 6.4 representing the different cohorts). This supports the findings of Wiegand *et al.* (2004) that not all recruitment has to be mass recruitment to allow long-term survival of trees. Rather, continuous recruitment is of major importance for maintaining and stabilizing shrub cover cycles.

The steep decline points to a simultaneous break-down of the shrub cohorts that constitute the build-up phase. The slow increase and steep decline of the shrub cover cycles is in agreement with the curve representing the relationship of community productivity over time in Watt's (1947) description of patch dynamics. In the break-down phase, size-frequency distributions are biased towards smaller shrubs (Fig. 6.4c). This indicates that larger shrubs are affected more strongly by mortality. In conclusion, we can reject the null-hypothesis that cyclical succession cannot emerge from a realistic patch-scale simulation model of the population dynamics of savanna woody species.

We suggest water availability as trigger and driver of the cycles, because more than 90% of the variation in shrub cover is explained by lagged shrub cover and annual precipitation. Shrub cover mainly depends on shrub cover in the previous year, but the only other important effect in the model is water availability. Individual water uptake translates into regrowth and therefore accounts for the difference in shrub size (which is related to shrub cover) between two years.

Precipitation has a stronger influence on shrub cover, the greater the shrub cover is in the previous year (Fig. 6.6). From the size-frequency distributions, we can derive that increases in shrub cover are primarily due to growth and only secondarily due to increased densities. Thus, larger shrubs are more susceptible to changes in precipitation than small shrubs. The underlying mechanism may be increased competition for water in dense populations of large shrubs where root system overlaps are common. Overlap of shrub root systems is increasing during the build-up phase of shrub cycles which is increasing the overall moisture requirements so that too little precipitation is of major importance for triggering the break-down phase. Apart from mediating competitive exclusion, precipitation falling below the drought threshold also contributes to break-down by inducing additional drought mortalities in established shrubs.

The importance of water availability for shrub cover is supported by the sensitivity analysis of SATCHMO where 7 out of 9 sensitive parameters were related

to soil moisture (Chapter 5). Sankaran *et al.* (2005) also show that in arid and semi-arid savannas with a mean annual precipitation of up to 650 mm, precipitation is the single most important factor determining the upper boundary of shrub cover for a given site. In other demographic bottleneck models, years with favourable rainfall also lead to shrub encroachment (*i.e.,* the peak of a successional cycle) in arid savannas (Sankaran *et al.* 2004). This phenomenon is mostly linked to even-aged stands of woody plants (Sankaran *et al.* 2004) which is consistent with the three-phase explanation presented here.

The importance of precipitation on the local scale as shown in this study does not support the common notion that climatic variables are primarily responsible for global-scale vegetation patterns whereas local to landscape-scale patterns are more often determined by local disturbances such as fire (Wu & Loucks 1995). In moist savannas, fire and herbivory may replace precipitation as the driver and trigger of successional cycles (Jeltsch *et al.* 2000; Sankaran *et al.* 2005). However, in semi-arid savannas, fire does not have a major influence on shrub cover cycles. This was also supported by the sensitivity analysis of SATCHMO where fire frequency was not among the significant variables to which shrub cover was sensitive (Chapter 5).

The consequence of our results for the management of encroached arid and semi-arid savannas is patience because a natural break-down phase with little woody cover will follow an encroached phase. However, this is not true if competition intensity is decreased through overgrazing. Thinning by cutting individual shrubs (Smit 2004) may help as long as competition remains strong enough to ensure a break-down under unfavourable precipitation conditions. Prescribed fires are unlikely to diminish shrub encroachment in arid savannas because shrub cover was not sensitive to fire frequency in the model. In the light of cycle durations of about 30 years, admittedly, waiting is not a motivating management option. In a patch-dynamic setting, large-scale spatial rotation systems of grazing areas could overcome these problems as long as natural grazing intensities are maintained.

In conclusion, we have shown cyclical succession for a semi-arid savanna patch with the spatially-explicit simulation model SATCHMO and have provided a three-phase mechanistic explanation of shrub cover cycles driven by precipitation. The next step will be to complement this temporal aspect of patch-dynamics with its spatial counterpart by scaling-up to the landscape scale. The smaller the spatial or temporal scale, the greater is the variability and non-equilibrium dynamics

dominate (Wu & Loucks 1995). There are two possibilities to obtain an equilibrium view, which both increase the scale of observation: averaging over time and/or space or redefining the equilibrium as some bounded range (sensu Wu & Loucks 1995). Here, the bounded range could be represented as maximum and minimum shrub cover over all simulations, *i.e.* 0.05 and 0.35, respectively. While averaging over time is relatively simple for the results shown in this study, averaging over space first necessitates the scaling-up to the landscape scale. A landscape-scale model of semi-arid savanna dynamics should consist of patches as they were set up in SATCHMO. If the spatial resolution corresponds to the grid size in SATCHMO (about 50 m), the temporal resolution should correspond to the significant time lag in the temporal autocorrelation analysis, *i.e.* about 30 years. This temporal resolution corresponds to the "break points" in scale-dependent spatial pattern analyses that aim at identifying domains of scale (*e.g.*, Milne 1988; Wiens 1989; Wiens & Milne 1989). Once the landscape-scale model is built, the results from SATCHMO can be used partly for parameterization and partly for validation of the large-scale model (see also Ludwig & Walters 1985). Finally, we will be able to investigate the conditions that constrain the applicability of the patch-dynamics mechanism for the explanation of both spatial and temporal savanna dynamics. However, with the establishment of the temporal component of patch-dynamics for arid and semi-arid savannas through the results from SATCHMO, a major step towards this end is made.

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7
Concluding discussion

The three-phase mechanism · Aim (1)

If tree-grass coexistence in savannas is maintained by the patch-dynamics mechanism (Gillson 2004; Wiegand *et al.* 2005; Wiegand *et al.* 2006), then cyclical succession should be observed at the patch-scale. The results presented in this dissertation are consistent with the hypothesis that precipitation-driven cyclical succession occurs in semi-arid savanna patches. In agreement with Wiegand *et al.* (2005; 2006), I suggest that cyclical succession proceeds in three phases: (1) initiation phase characterized by mass recruitment of shrubs under favourable environmental conditions, possibly ameliorated by facilitative effects, (2) build-up phase where the shrubs of a cohort increase in size so that root system overlap becomes greater and competitive pressure intensifies, and (3) break-down phase with die-back of the shrub cohort due to the interaction of high competitive pressure and unfavourable conditions affecting large shrubs with greater intensity than smaller ones. During these three phases, the predominating mode of interaction between woody species shifts from facilitative to competitive. The three-phase explanation is consistent with the claim raised by Chesson *et al.* (2004) that covariance between environment and competition is an important prerequisite of coexistence in savannas. During environmentally favourable periods, the intensity of intra-specific competition has to increase for the favoured life form to promote coexistence (Chesson *et al.* 2004), such as during the build-up phase of the successional cycles.

Support for the three-phase cycle & resolution of patch-dynamics · Aims (2 & 3)

The corroboration of this cyclical succession procedure was achieved through the application of a multitude of spatial and non-spatial approaches, such as field observations, a field experiment, spatial and conventional statistics, and the development of new methods including the spatially explicit, individual-based simulation model SATCHMO. To identify the necessary extent of the grid SATCHMO is based on, a new method was developed for the determination of patch size based on spatial patterns of shrub canopies or root systems and the Neyman-Scott

cluster process (Chapter 4). The new method is useful for the empirical derivation of patch sizes in the patch-dynamics paradigm and yielded a patch diameter of up to 40 m for the study area. Therefore, the side length of the model grid in SATCHMO was set to 50 m (including a buffer for edge effects). SATCHMO was designed with particular attention to the recognized importance of belowground interactions in savannas (Vila 1997). This includes its unique characteristic of spatially explicit root growth allowing for the investigation of different competition scenarios (Chapter 5). Another distinctive feature of SATCHMO is its successful validation with a broad array of independent field and literature data demonstrating its close link to reality (Chapter 5).

The autocorrelation analysis of 100 time series of shrub cover, that were simulated with SATCHMO, confirms the existence of cycles at the patch-scale and reveals the duration of a typical cycle (33 years, Chapter 6). The three-phase explanation is supported by the match of cycle duration and median age at death of simulated shrub (40 years). More support is provided by the shift of size-frequency distributions towards larger simulated shrubs during the build-up phase of cycles and towards smaller shrubs during break-down (Chapter 6).

In addition to the simulation results, the analyses of field data also provide evidence for the three phases of successional cycles. The hypothesis of mass recruitment in the initiation phase of cyclical succession is supported by the aggregation of small (*i.e.*, young) shrubs at the field site (Chapter 2). The most probable reason for spatial aggregation at young age in the study area is aggregated seed dispersal (K. Meyer, unpublished observations) combined with facilitation by the parent shrub (Belsky 1994; Holzapfel & Mahall 1999; Münzbergova & Ward 2002). Mass recruitment events occur only during occasional favourable conditions. Seeds will then cluster at those sites that temporarily become suitable for establishment. Facilitation may enhance the quality and number of such regeneration sites.

The agreement of the mode of root length distributions with the scales of negative autocorrelation and regular point patterns indicates that competition intensifies when root systems start to overlap (Chapter 2). I suggest this increase in overlap as mechanism behind the build-up phase of the successional cycle. Parallel to increased root overlap, competition-induced mortality will become more probable and thereby provide the prerequisite of the break-down phase of the successional cycle.

Although spatial point pattern analysis detected overall aggregated shrub patterns at the field site, the competitive effect on shrub mortality was revealed by decreasing spatial aggregation with shrub age (Chapter 2, where size is used as a proxy for age). Hence, a temporal component (here age) should be included in spatial analyses that aim to discover competitive effects on mortality masked by overall aggregation of individuals (Wolf 2005). The competitive effect on shrub size was more clearly exposed by negative spatial autocorrelation of shrub canopy diameters and a positive relationship between distance to nearest neighbours and combined shrub size (Chapter 2). Spatial pattern analysis approaches can be more time-efficient than experimental approaches for the identification of competition in arid areas. The slow growth rates of savanna shrubs in arid areas (Chapter 2) may have been the reason for the non-significant or only marginally significant differences between shrubs whose competitors were experimentally removed and control shrubs (Chapter 2). Spatial pattern analyses provide only indirect evidence of competition (or other interactions) while experiments can test the prevalence of competition directly. However, if several different spatial analysis approaches generate the same result as in this case and there are doubts about the sufficient duration of an experiment, drawing a conclusion in line with the spatial analysis results is appropriate. Hence, if long-term competitor removal experiments are not possible, the simultaneous application of several different spatial analysis techniques may be a valuable and time-saving alternative.

The assumption that, during the break-down phase of the successional cycle, large shrubs have a greater probability to die earlier, is in agreement with the morphometric field study of *A. mellifera* shrubs after fire: Large shrubs were more susceptible to fire and had relatively smaller regrowth indicating the presence of senescence effects in the species (Chapter 3). Note that, contrary to the conventional definition of senescence (Yoshida 2003), in this context, senescence is not restricted to age-related physiological dysfunctions but also applies to size-related dysfunctions (Mencuccini *et al.* 2005). Cohort senescence has been shown to be a predisposing cause of *Acacia* mortality (Young & Lindsay 1988) preparing the ground for an ultimate trigger of cohort mortality such as unfavourable environmental conditions (see next section). Since SATCHMO does not include a senescence effect explicitly, the break-down phase is likely to be even steeper in reality than in the simulated time series.

The trigger of the break-down phase · Aim (4)

The break-down of the shrub cohort(s) needs a trigger that interacts with the mortality of the shrubs. Candidates for the trigger are the four classic key-factors determining woody cover in savannas, *i.e.*, precipitation, nutrients, fire, and herbivory (Frost & Robertson 1987; Sankaran *et al.* 2004). However, if natural grazing intensities are exceeded, grazing commonly leads to increases in shrub cover, *i.e.*, the opposite of a break-down (Skarpe 1990; Perkins & Thomas 1993). Thus, grazing is more likely to start and/or extend the duration of the build-up phase because it releases woody species from the competition with grasses. Contrarily, browsing could theoretically reduce shrub cover. However, SATCHMO is based on the major encroaching species *Acacia mellifera* which is not much affected by browsing because its multitude of prickles. Browsers prefer grass over *A. mellifera* leaves when it is available (D. Ward, pers. comm.). Hence, their detrimental impact on *A. mellifera* only sets in when grass cover is reduced during drought years. Thus, browsing can only be a secondary trigger of break-down depending on precipitation.

Nutrient dynamics are coupled to soil moisture dynamics (Scholes & Archer 1997) making a separate consideration of these two factors difficult. However, nutrient enrichment has been found under the canopies of many savanna woody species (Mordelet *et al.* 1993; Belsky 1994; Evans & Ehleringer 1994; Wiegand *et al.* 2005), especially under leguminous *Acacia* species capable of nitrogen fixation in root nodules (Bernhard-Reversat 1982). Nutrient enrichment can have a facilitative effect on herbaceous species (Callaway 1995) whose subsequent increase can lead to increased competitive pressure on the 'nurse tree' (Scholes & Archer 1997; Ludwig *et al.* 2004). This whole process can be seen as a possible negative feedback loop of nutrients on tree vitality and therefore has the potential to impair the growth and, to a lesser extent, vitality of woody species. However, the negative feedback will be too slow to induce the steep declines postulated for the break-down phase. Nutrients may contribute only indirectly to starting a break-down by being linked to soil moisture dynamics (see below) (Scholes & Archer 1997).

Fire is a promising candidate for triggering the shrub cohort break-down because it is a discrete event in time that has the potential to lead to high mortalities in woody species. However, this is only true for moist savannas, where grass cover is sufficiently high to fuel frequent fires of high intensities (Higgins *et al.* 2000). In the semi-arid study area, we found high resprouting ability of *A.*

mellifera shrubs after fire and very low fire mortalities (9%, Chapter 3). This is supported by the sensitivity analysis of SATCHMO, where fire-frequency was not among the significant parameters retained in the regression model (Chapter 5). This indicates that, even if a fire occurs in a semi-arid savanna, it is unlikely to have the potential to trigger the break-down of a whole shrub cohort.

Hence, herbivory, nutrients, and fire are not likely to initiate shrub cohort break-down in semi-arid savannas leaving precipitation as the most promising trigger. Among the significant parameters retained in the regression model of the sensitivity analysis of shrub cover in SATCHMO, 7 out of 9 were moisture-related (Chapter 5). The regression analysis of 100 simulated shrub cover time series generated a significantly positive relationship between precipitation and shrub cover (Chapter 6). This establishes the importance of precipitation for shrub cover dynamics and substantiates the role of precipitation as driver of successional cycles in semi-arid savannas. The significant interaction between lagged shrub cover and precipitation retained in the regression model emphasizes the particular importance of precipitation for the break-down phase of the cycles: The greater the shrub cover is in the previous year, the greater is the impact of precipitation (e.g., droughts) on current shrub cover (Chapter 6).

Demographic bottlenecks and competition · Aim (5)

In the sensitivity analysis of SATCHMO, the only significant parameter related to shrub demography was browsing mortality of seedlings presenting a serious demographic bottleneck in SATCHMO (Chapter 5). This is supported by the bimodal age-at-death distribution of shrubs in SATCHMO where shrubs younger than 6 years represent 80% of the total number of dying shrubs (Chapter 6). On the other hand, empirical evidence and model results suggest that competition is a major structuring force in temporal and spatial shrub population dynamics (Chapters 2, 5 & 6). In agreement with Sankaran *et al.* (2004), this shows that both competition and demographic bottlenecks are important for the explanation of tree-grass coexistence in savannas. However, following the results of the sensitivity analysis of SATCHMO, competition for soil moisture seems to play a more crucial role for shrub cover cycles than demographic bottlenecks (Chapter 5). This is supported by the results from the regression analysis of simulated shrub cover time series, where the dependence of shrub cover on precipitation increased with shrub cover (and therefore with intra-life form-competition, Chapter 6). With respect to determining savanna dynamics, competition and demographic bottlenecks should

be complemented with the remarkable influence of environmental conditions, particularly temporally and spatially variable precipitation (Chesson *et al.* 2004). Precipitation is involved in both mechanisms - in competition as a limiting resource and in demographic bottlenecks as environmental trigger - but also has an independent effect as disturbance agent causing drought mortalities (Chapter 5).

Management of shrub encroachment · Aim (6)

In the light of the results presented here, management of the growing ecological-economic problem of shrub encroachment is difficult because shrub encroachment constitutes a natural phase (the build-up phase) of cyclical succession which is mainly sensitive to moisture parameters whose manipulation is costly and inefficient (Chapter 5). Hence, I suggest patience until the onset of the break-down phase or large-scale spatial rotation schemes that maintain natural grazing intensities in those patches of the patch-dynamic mosaic that are in the grass-dominated phase. I have shown that the successional cycles and especially the break-down phase are driven by precipitation so that encroachment managers could derive the onset of the break-down phase from observations of rainfall dynamics. Grazing and particularly overgrazing leads to the start of the initiation phase or an extended duration of the (naturally encroached) build-up phase. The suggested management option is consistent with the advice to reduce grazing intensities in high rainfall years to not weaken the competitive effect of grasses on woody species (Müller *et al.* in press). SATCHMO provides a suitable tool for testing and comparing the efficiency of these or other management scenarios such as tree thinning or prescribed burning.

Outlook

The results from this dissertation have underlined the importance of competition for successional cycles, but the relative importance of different competition mechanisms remains to be quantified. SATCHMO is ideally suited for an extension that aims to compare and enlighten the relative importance of different competition and facilitation scenarios, including mixed competition scenarios where the mode of competition switches depending on environmental conditions. To establish the relative effects of natural shrub encroachment and shrub encroachment caused by overgrazing, explicit grazing scenarios could also be incorporated into SATCHMO.

The existence, duration, phases, and drivers of successional cycles in semi-arid savanna patches have been established and discussed in this dissertation. The next step will be to assemble a landscape-scale mosaic of savanna patches with cyclical successions in a second simulation model. The results of the present dissertation can serve to parameterize the landscape-scale model in a scaling-up procedure. For instance, if the spatial resolution of the landscape-scale model is based on the patch sizes determined in this study (about 50 m), then the temporal resolution should be equal to the duration of cycles identified in this study (about 30 years). Thereby, the importance of spatial and temporal scales for the explanation of tree-grass coexistence in savannas is acknowledged (*cf.* Levin 1992). By successfully demonstrating the temporal component of patch-dynamics for a semi-arid savanna, this dissertation has reached the first milestone on the way towards establishing patch-dynamics with the help of simulation models as the unifying mechanism explaining the coexistence of grassy and woody species in savannas.

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Summary

Many mechanisms have been proposed to explain tree-grass coexistence in savannas but empirical evidence is equivocal. Patch-dynamics is a new, potentially unifying, scale-explicit approach to explain savanna dynamics and the ecological and economic problem of shrub encroachment in arid and semi-arid savannas. A patch-dynamic savanna consists of a spatial mosaic of patches that maintain a cyclical succession between woody and grassy dominance spatially asynchronously. To achieve an understanding of ecological patterns at the landscape-scale, underlying mechanisms should be studied at smaller scales.

Hence, the spatially explicit individual-based simulation model of a semi-arid savanna patch SATCHMO was developed, implemented, and successfully validated with field and literature data. Spatial pattern analyses of field data from a semi-arid savanna site in the Kalahari thornveld, South Africa, and a competitor removal experiment were carried out to support the simulations. Cyclical succession emerged from the analysis of shrub cover time series simulated with a realistic parameterisation of SATCHMO. I propose a three-phase concept to explain the successional cycles: (1) initial phase with mass recruitment of shrubs, (2) build-up phase with shrub cohort growth, and (3) break-down phase with simultaneous and size-dependent death of most shrubs in the cohort. The three-phase concept is supported by empirical and model-based evidence, including the match of age at death of simulated shrubs and duration of a cycle, the shift of simulated size-frequencies during the cycle, the match of median root length and the scale of regular shrub patterns, and the evidence for senescence effects in large shrubs at the field site.

Soil moisture was a much more important driver of successional cycles (and a trigger of the break-down phase) than fire because fire was not among the 9 significant parameters of the sensitivity analysis of SATCHMO whereas 7 soil moisture related parameters were significant. Fire did only cause little shrub mortality at the study site and there was a significantly positive relationship between annual precipitation and shrub cover in SATCHMO. It can be inferred from spatial point pattern analyses that during a successional cycle, the mode of interaction between shrubs is shifting from facilitation to competition. Although spatial pattern analyses are only indirect methods for inferring competition, the application of several different spatial pattern analysis methods should be

preferred over an experimental approach if time is limiting. Competition is more important than demographic bottlenecks for the explanation of tree-grass coexistence in savannas.

In cyclical succession, shrub encroachment is a natural, transient phase (the build-up phase). Hence, the most promising management of encroached areas is patience or a large-scale rotation system of rangelands in which case rangeland managers should take the spatial and temporal extent of a patch cycle into account. The spatial extent of an encroached patch can be determined according to a new method proposed in this dissertation (patch diameter in the study area: 40 m) while the duration of the cycle or its phases can be obtained from the analysis of time series generated with SATCHMO (here: 33 years). The extent of a patch cycle can also be used as spatila and temporal resolution of a second simulation model at the landscape-scale that will be parameterised based on the cyclical succession results obtained with SATCHMO. The landscape-scale model will allow the investigation of the spatial dimension of patch-dynamics in savannas. With the demonstration of precipitation-driven cyclical successions, this dissertation has established the core of patch-dynamics for a semi-arid savanna and provided a well supported mechanism for its explanation.

Zusammenfassung

Der Koexistenzmechanismus von holzigen Pflanzen und Gräsern in Savannen ist trotz einer Vielzahl aufgestellter Hypothesen noch immer ungeklärt, denn empirische Belege für die Hypothesen sind uneinheitlich. *Patch-dynamics* ist ein neuer skalen-expliziter Ansatz zur Erklärung von Savannendynamik und dem ökologisch-ökonomischen Problem der Verbuschung von ariden und semi-ariden Savannen, der das Potenzial hat, viele der vorgebrachten Hypothesen zu einem übergreifenden Mechanismus zu vereinen. Eine durch *patch-dynamics* gekennzeichnete Savanne besteht aus einem Mosaik von Patchen, in denen eine zyklische Sukzession zwischen Gras- und Holzpflanzendominanz räumlich asynchron abläuft. Zum Verständnis ökologischer Muster auf der Landschaftsebene sollten zunächst die zugrunde liegenden Mechanismen auf kleineren Skalen untersucht werden.

Daher wurde in dieser Dissertation das räumlich explizite individuenbasierte Simulationsmodell SATCHMO (SAvanna paTCH MOdel) für einen semi-ariden Savannenpatch entwickelt, implementiert und mit Feld- und Literaturdaten erfolgreich validiert. Um die Simulationen zu unterstützen, wurden die räumlichen Muster von Felddaten aus einer semi-ariden Savanne im Kalahari Dornbuschgebiet in Südafrika analysiert und ein Strauchkonkurrenz-Experiment durchgeführt. Bei realitätsnaher Parameterisierung von SATCHMO ergaben sich zyklische Sukzessionen aus der Analyse von simulierten Strauchdeckungszeitreihen. Ich schlage zur Erklärung der Sukzessionszyklen ein Drei-Phasen-Konzept, bestehend aus Anfangsphase mit Massenreproduktion der Sträucher, Aufbauphase mit simultanem Strauchkohortenwachstum und Zusammenbruchphase mit Massensterben vor allem der größeren Sträucher, vor. Das Drei-Phasen-Konzept wird durch modellbasierte und empirische Untersuchungen gestützt, z.B. durch Übereinstimmung der Lebenserwartung der simulierten Sträucher und der Zyklusdauer, durch Strauchgrößenverschiebung während eines Zyklus', durch Übereinstimmung der mittleren Wurzellänge mit der Skala regelmäßiger Strauchmuster und durch Hinweise auf Seneszenzeffekte bei größeren Sträuchern im Untersuchungsgebiet.

Bodenfeuchte hat eine wesentlich größere Bedeutung als Auslöser der Sukzessionszyklen (vor allem der Zusammenbruchphase) als Feuer, denn während sieben der neun signifikanten Parameter der Sensitivitätsanalyse von SATCHMO

Bodenfeuchteparameter waren, gehörte Feuer überhaupt nicht dazu. Darüber hinaus verursachte Feuer im Untersuchungsgebiet nur niedrige Strauchmortalität und der Jahresniederschlag hing in SATCHMO signifikant positiv mit der Strauchdeckung zusammen. Aus der räumlichen Analyse empirischer Strauchmuster lässt sich ableiten, dass sich während des Ablaufs eines Sukzessionszyklus' die dominierende Wechselwirkungsform innerhalb der Sträucher von Begünstigung (*facilitation*) zu Konkurrenz verschiebt. Methodisch ergibt sich für die Demonstration von Konkurrenz, dass die Anwendung von mehreren verschiedenen räumlichen Analysemethoden einem Experiment vorzuziehen ist, sofern Langzeitexperimente nicht möglich sind, obwohl räumliche Analysen nur indirekte Nachweise von Konkurrenz liefern können. Für die Erklärung von Gras-Holzpflanzen-Koexistenz in ariden Savannen ist Konkurrenz ein wichtigerer Faktor als demographische Flaschenhälse.

Für das Management von verbuschten Flächen ergibt sich, dass man Verbuschung als natürlicher Phase in Sukzessionszyklen (Aufbauphase) am effektivsten mit Geduld oder großräumiger Rotation der Weideplätze begegnet. Dabei sollten sich Landwirte an der räumlichen und zeitlichen Ausdehnung eines Patchzyklus' orientieren, die sich mit Hilfe einer in dieser Arbeit vorgestellten Methode (Patchdurchmesser im Untersuchungsgebiet: 40 m) bzw. mit einer Analyse der von SATCHMO generierten Zeitreihen (hier 33 Jahre) bestimmen lassen. Die Ausdehnung eines Patchzyklus' sollte auch der räumlichen und zeitlichen Auflösung eines zweiten Simulationsmodells auf Landschaftsebene zugrunde liegen, das im nächsten Schritt auf Basis der in dieser Dissertation gewonnenen Erkenntnisse zur zyklischen Sukzession parameterisiert werden soll. Während diese Dissertation mit der Demonstration von regenbestimmten zyklischen Sukzessionen den Kern von *patch-dynamics* für semi-aride Savannen bestätigt und mechanistisch untermauert hat, wird durch ein Modell auf Landschaftsebene auch der Nachweis der räumlichen Dimension von *patch-dynamics* in Savannen möglich.

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Selbständigkeitserklärung

Ich erkläre hiermit, dass ich die vorliegende Arbeit selbständig und nur unter Verwendung der angegebenen Hilfsmittel und Literatur angefertigt habe.

Dabei gestaltet sich der Anteil der Koautoren der Manuskripte, die auf Grundlage der Kapitel 2 bis 6 schon erschienen sind, zur Publikation eingereicht wurden oder zur Publikation vorbereitet werden, folgendermaßen:

Für alle Kapitel habe ich die Daten selbständig statistisch analysiert und nach Diskussion der Ergebnisse mit den jeweiligen Koautoren die Manuskripte und Kapitel selbständig erstellt.

Bei der Aufnahme der Daten in Kapitel 2, 3 und 4 haben mir D. Ward und A. Moustakas geholfen, das Konkurrenz-Experiment in Kapitel 2 wurde von D. Ward aufgebaut und durchgeführt.

Das Simulationsmodell, das in Kapitel 5 und 6 beschrieben und analysiert wird, habe ich nach Diskussionen mit K. Wiegand selbständig konzeptionalisiert, programmiert und analysiert.

Jena, den 12.05.2006

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EDUCATION

2003 to 2006 **PhD at Friedrich-Schiller-University Jena, Germany, Institute of Ecology, Spatial Ecology Lab**
PhD thesis: "Cyclical succession in semi-arid savannas revealed with a spatial simulation model" supervised by Kerstin Wiegand (Jena, Germany) and David Ward (Pietermaritzburg, South Africa)

1997 to 2003 **Diploma Studies at Philipps-University Marburg, Germany, Department of Biology**
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Degree "Diplombiologin": 1.0 with distinction, best diploma of the graduation year (scale: 1.0=maximum, 4.0=minimum for passing)

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SCHOLARSHIP

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OTHER WORK EXPERIENCE

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LIST OF PUBLICATIONS

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In press	Moustakas A., Guenther M., Wiegand K., Mueller K.H., Ward D., **Meyer K.M.** Size class distribution of *Acacia erioloba* mortality: the middle class shall die! J Veg Sci.

PUBLISHED ABSTRACTS (POSTERS):

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2004	**Meyer K.M.**, DeBell D., Harms W., Gerstenlauer J., Wiegand K. Forests on diet: Spatial analyses of mortality in tree plantations. Verhandlungen der Gesellschaft für Ökologie, Band 34.
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TALKS:

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INVITED TALKS:

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